THE IMPACT OF MUIRBURNING ON LICHEN DIVERSITY

Gwilym Matthew Davies

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Name of Candidate **Gwilym Matthew Davies**

Address [redacted]

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The use of fire as a management tool on moorlands is a practice with a long history. Primarily carried out to maintain a monoculture of young, vigorous growth *Calluna* to provide higher quality grazing for sheep, deer and grouse muirburning has a profound effect on the ecology and species composition of moorlands. The overriding influence on the ecology of heathlands is the life-cycle of *Calluna vulgaris* from the early pioneer phase through the building and mature phases to the degenerate phase. Lichen diversity is largely controlled by the life cycle of *C. vulgaris*. The process of burning interrupts the natural life cycle of *Calluna* preventing it moving into the mature and degenerate phases. From the early building phase onwards *Calluna* begins to greatly influence the microclimate below it canopy creating darker, moist conditions which favour the growth of pleurocarpous mosses over lichens and sees the latter largely replaced with the exception of a few bryophilous species. Muirburning largely aims to prevent progression to the mature and degenerate phases and thus to period traditionally seen as of high lichen diversity. However it maintains areas free from the overriding influence of *Calluna* where lichens may be able to maintain higher diversity than beneath the *Calluna* canopy.

One hundred quadrats were completed on the moorlands of the National Trust for Scotland Mar Lodge Estate with the aim of quantifying and explaining changes in lichen diversity. 37 different burns were investigated as well as 26 unburnt sites. Analysis of the data was carried out using regression analysis and DCA. The results indicate that lichen diversity increases following burning but declines underneath the closed *Calluna* canopy. Mats of pleurocarpous mosses largely replaced lichens in older stands with only corticolous species showing any increase in this phase. There exists however significant differences between different communities with lichens in the second area studied being both more diverse and maintaining their abundance into the building phase, the drier conditions allowing them to fill the niche normally held by pleurocarpous mosses. Key factors in controlling lichen diversity were shown to be the time since fire and soil moisture although the latter may be linked to the changing dominance of *Calluna* and the influence of its microclimate.

Key Words: *Calluna vulgaris*, life-cycle, fire, heathland, regeneration, soil moisture

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GENERAL INTRODUCTION

Much literature exists on the ecology of *Calluna* heathland and the process and impacts of muirburning. This is thanks in no small part to the economic and social importance of moorlands; both in terms of agriculture and the sporting activities they support. Of particular importance is hunting and it was after the disastrous falls in grouse populations in the early part of this century that research gathered pace starting with a public enquiry by the House of Lords. The association of moorlands with grouse shooting and deer stalking has no doubt led to many of the reservations and prejudices people have about the process. Despite continuing research there remains a negative attitude towards heathlands amongst many people who see them merely as something to be reforested and fail to realise the importance of these communities in their own right. Much research carried out has focused in particular on the life-cycle and regeneration of *Calluna* and on the ecology of vascular plants. Relatively little attention has however been paid to the lower plants and this paper seeks to redress this imbalance somewhat. The first paper, the literature review, examines existing knowledge about the history and ecology of heathlands, the process of muirburning and the impact this has on their ecology. It pays special attention to the potentially important role that lichens play within this community. The practical paper was carried out at the Mar Lodge Estate near Braemar and sought to quantify changes in lichen diversity. One hundred quadrats were carried out examining burns of several ages as well as unburnt population. Several statistical analyses were carried out on the data collected with the aim of discovering how and why lichen diversity changes following burning.

LITERATURE REVIEW

ABSTRACT

The ecology of managed heathlands are dominated by two things: the life cycle of *Calluna vulgaris* and the process of muirburning. Frequently viewed as an unnatural, undesirable result of human impact on the landscape and emblem of deforestation moorlands are in fact on a European scale a relatively rare and valuable habitat. Heathlands are unusual due to the dominance across all there range of a single species: *C. vulgaris* despite the variation that exists in this habitat. It is this species that largely controls the ecology of heathlands. Much work has been done examining the impact this has on the composition and regeneration of vascular plants and examining how variations in vegetation and firing processes effect the regeneration pathways of the community following burning. Lower plants have largely only been referred to in passing. Heathlands are an important community for lichens frequently having a diversity found in few other places. A number of lichen species are limited to these areas. Lichen diversity on heathlands is largely controlled by the life cycle of *Calluna* and the influence this exerts on other species, the damp and dark microclimate it exerts beneath its canopy is well documented. In relatively young sites high lichen diversity can be reached with genus *Cladonia* being particularly important. Some authors suggest that the opening canopy of the degenerate phase may also support a high diversity of species particularly with colonisation by corticolous species. Muirburning is important in that it maintains a patchwork of habitats of different ages which allows all stages of *Calluna* to exist on many moorlands meaning there is a difference between the α diversity of an individual burn and its β diversity. Regeneration speed of *Calluna* following burning is influenced by a number of factors and including the age of the vegetation and the intensity of the fire. These factors may also influence eventual lichen diversity as they control the amount of time when there is a habitat suitable for terricolous lichen colonisation.

1. INTRODUCTION

This paper aims to give an introduction to the study of moorlands, focusing in particular on the role and dynamics of lichens within these communities. To this end several areas will be examined. Firstly a description of heathland communities will be given looking at their distribution, communities and place within the NVC system, their key component species as well as an overview of their history and formation. It will then be possible to go on to examine the ecology of heathlands examining the factors that control lichen diversity. The second chapter will examine heathland management techniques and systems including an examination of the process of muirburning while the third chapter will examine the impacts of management and look at the process of regeneration, secondary succession and the effects of these on lichen diversity.

2. THE NATURE AND HISTORY OF MOORLANDS

2.0 Location

Upland vegetation communities cover approximately one third of the British Isles (around 37,110 km^2) and roughly 25,140 km^2 in Scotland and consists mostly of sub montane dwarf shrub heath. It is a largely anthropogenic community resulting from the clearance of natural forests and their replacement with native shrub species. Reversion to a forest state has been prevented by management practices including burning and grazing (Ratcliffe & Thompson 1988). Natural dwarf shrub heaths are found in the UK above the treeline and in the Cairngorms in the altitudinal range 700-1100 m asl. The lower limits of *Calluna* varies however through Scotland at 550 m Sutherland and 200-300 m in the Orkneys and Shetland. *Calluna vulgaris* normally dominates in the low-alpine zone and *Vaccinium myrtillus* at higher altitudes as well as a number of other dwarf shrub species. Grasses and sedges are also common and lichens and mosses may frequently also play an important role (Cairngorms Partnership).

Upland (anthropogenic) heathland includes a range of dwarf shrub heathlands including dry and wet heaths. It is usually found at the upper edge of enclosed agricultural land and below the montane zone. It can be grouped together with acid grassland and blanket bog in the category "moorland." Heathland is generally found on acid, nutrient poor soils with annual precipitation greater than 100cm yr $^{-1}$and as has been stated is primarily derived from former woodland and scrub. Blanket bog cover generally increases westwards and this region also contains some of the more bryophyte rich communities while lichen heaths are favoured by the more continental conditions found in the East (Cairngorms Partnership, Ratcliffe & Thompson 1988). Investigations to put accurate figures to the extent of heather moorland have been carried out by Bradbury *et al.* (1990).

Despite its anthropogenic background upland heath is of conservation interest being highly distinctive and largely confined to the UK and the western seaboard of Europe (Cairngorms Partnership) a fact which is often overlooked in this country.

2.1 The History of Moorlands

The history of anthropogenic interference in the landscape is a long one. There is evidence from pollen data that as far back as the Mesolithic humans were modifying their environment and burning small areas of the forest to open up clearings. This not only allowed the growth of food plants such as *Rubus saxatilis* and *Corylus avellana* but also provide grazing for prey species (Smith 1992). Peat cores from the Black Ride Brook site show large amounts of microscopic charcoal, associated with a decline in arboreal pollen and a steep rise in the amount of grass species between 7700 and 6300 BP. The presence of *Calluna*, *Melampyrum*, *Plantago lanceolata* and *Ranunculaceae* further support the idea of deliberate disturbance (Caseldine & Hatton 1993). These early modifications were however small in scale and probably reversible, although there is evidence that some areas of chalk downland in the Yorkshire Wolds date back to this period. The first major evidence for large-scale human modification of the environment comes with the Elm Decline. At this point around 4000 BC, around the time of the spread of agriculture into Northern Europe, there is dramatic drop in the abundance of *Ulmus* associated in Britain and Ireland with an increase in agricultural herbs and indicators of disturbance. Dutch Elm Disease is the most likely explanation for this remarkable decline but pollarding of elms for fodder, and selective clearance as elms grew on the most promising agricultural land were likely to also have had an impact (Simmons 1990). It is highly possible that the combination of early forest clearance and a downturn in environmental conditions could well have led to the large scale onset of peat formation, blanket bog and heath development as early as the Neolithic (Bell & Walker 1992). Destruction of the natural forest continued through the Neolithic and Bronze Ages during the latter period extending to high altitudes as a milder climate allowed for arable agriculture at higher elevations than today. Climatic downturn later caused the initiation of blanket bogs in many of these previously fertile areas. Activity increased in the Iron Age as axes and ploughs became cheap and more efficient. Rackham (1990) estimates that half of the wildwood of England had been cleared by 500BC. The use of fire and grazing by goats and cattle largely put paid to any chances for regeneration.

Extensive deforestation occurred through the Roman period and on into historical times where it accelerated to provide timber for the construction of ships and for fuel for smelting iron-ore. English woods were largely depleted by Elizabethan times and the destruction moved northwards into Scotland. Clearance in the upland paved the way for first cattle grazing and later for sheep. The eighteenth century in Scotland saw the introduction of cheviot sheep, large flocks of which required a smaller workforce leading to the infamous Highland Clearances. Large areas of woodland were destroyed to stop peasants from re-building their burnt-down homes. As sheep are selective grazers the uplands rapidly deteriorated in grazing quality due to the invasion of woody species and pests such as *Pteridium aquilinum*. Burning therefore became an increasingly frequent management technique and served the added purpose of encouraging the growth of young more nutritious shoots. British heaths therefore have a history of regular burning from 1800 onwards. Shepherds adopted a ten year burning rotation with every part of their moorland holding being fired once every ten years. Techniques however changed especially as landowners began to appreciate the sporting value of red grouse and many moors came to be managed for this sole purpose from 1850 onwards. Game keepers discouraged burning as better shooting was to be had when the birds were flushed out of long heather by beaters or dogs. A rapid decline in the number of birds took place from 1872 and 1873 and was attributed to infection by trichostrongyle threadworm. A committee of enquiry set up to study the problem however laid the ultimate blame at the hands of poor management practice and it was recommended that burning on rotation should be re-establish to control the worm. It now seems likely however that infection was a symptom rather than a cause of low population numbers which was caused ultimately by a lack of suitable habitat. Correlation’s can be drawn between population size and the proportion of pioneer and building *Calluna* (see below), drawing attention to the need for a carefully managed burning programme. It has also been shown that a patchwork of different aged heather is preferable to large even aged stands and therefore many smaller fires are preferable to a few larger ones. Large fires may however be acceptable where the aim is to provide grazing for sheep and deer (Gimingham 1972, Rackham 1990).

Management of moors for grazing and sport still plays an important part in the livelihood, ecology and environment and upland Britain at a time when many of the traditional estates are facing financial difficulties. Manpower for management is in short supply and traditional hill-sheep farming is in crisis, especially following the outbreak of foot and mouth disease. Management practice varies from place to place but in general many attempt to follow the traditional burning cycle of firing an area every 12-15 years. This practice is however threatened not just by the profitability if the economy it supports but also from increasing pressure to cease burning and allow the large-scale regeneration of woodland. In Scotland large areas of heather moorland have been lost since the 1940's, mainly to unimproved grassland and coniferous plantation, with decreases of 10-25% lost throughout Grampian, Tayside and the Highland regions (Cairngorms Partnership).

Bardgett *et al.* (1995) state that there are large areas of heather in Wales and England showing suppression due to poor management.

It therefore appears that our moorlands face a period of transition and an understanding of their ecology and value is imperative. It is also important to keep in mind the history of moorlands and to remember that they have been an integral part of our landscape for much longer than most people imagine. They also contain a number of important and in some cases rare species and communities just as deserving of protection than any other. Muirburning and heathland management gets a bad press however due to its links with upper class sporting activity, social exclusion and what in some corners is viewed as wanton environmental damage. While there is undoubtedly a need to encourage the regeneration of forest in many areas while doing this one should not gloss over the importance of moorlands and the integral part of our landscape which they form. Sydes and Miller (1988) are right to state that heather moorland is an integral part of the British upland landscape and supports a unique community of plants and animals. Simmons (1990) however argues that the artificial nature of moorlands calls for a reassessment of their importance and argues that the concepts of the World Conservation Strategy places emphasis on the importance of allowing woodland to regenerate. This however ignores the economic, visual and conservation value of moorlands. In my opinion, unlike Simmons the fact that the long history also goes some way to legitimising their existence and places emphasis on their importance as Cultural Landscapes with an important ecology, history and archaeology of their own.

In terms of lichens heathland plays an important role and is a key habitat with many species only found in such communities. The lower plants including lichens and bryophytes tend to get a bit of a raw deal and are species which are neither particularly recognisable to or cared about by the general public and many ecologists. The richness of moorland lichen communities are an important aspect of this ecosystem and something which has not been studied in any particular detail and references to them in studies of vegetation dynamics are frequently brief. This study therefore aims to fill a gap in our knowledge and provide an insight into the effects of management on lichen communities.

2.2 Moorland Ecology

British heathlands are unusual in that throughout their entire range, in particular on drier soils, they are dominated by a single species: *Calluna vulgaris*. In all but the wettest heaths *Calluna* is present and in the vast majority it will be dominant. There are a number of other species commonly associated with heathlands which may be represented as associates, co-dominants and in some areas may even become dominant at the expense of *C. vulgaris*. Despite this heaths, as Gimingham (1972) points out, represent possibly the best example of the dominance of one species throughout a considerable range of habitat conditions and community compositions. As has been stated earlier, historical factors and the response of *Calluna* to management largely explains this dominance as well as the ecology of *Calluna* itself. Heathlands are frequently largely oligotrophic (nutrient poor) and this combined with management practice leads to them being relatively species poor and allows one species to attain dominance. The fact that *Calluna* significantly modifies its environment, by creating a dark moist microclimate beneath its canopy and through the leachates released from its slow decomposition which encourage podzolisation, only serves to reinforce this trend. Mallik (1986) studied in detail the way in which unburnt Calluna increased interception and evapotranspiration even though soils below unburnt canopies were damper. Temperatures at the ground surface were also found to be lower at these sites.

The dominance of *Calluna* in heathland communities and the influence it exerts means that the ecology of heathlands to some extent becomes the ecology of *Calluna*, which perhaps explains some of the failure to examine the trends of other species groups such as lichens. The emphasis on *Calluna* is further assured by the interest in maintaining large populations of grouse which requires adequate management of the heather (Gimingham 1972). McVein and Lockie (1969) identified nine key categories of heather moorland which although updated by the NVC[*] system is still a useful general summary:

i. Pure heather sward with a sparse growth of mosses and lichens.
ii. Damp heather moor with *V. myrtillus, Empetrum nigrum* and deep moss (NVC H12).
iii. Dwarf heather sward with a variety of other shrubs (NVC has broken this category up into specific communities).

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[*] National Vegetation Classification

iv. *V. myrtillus* heaths with a few other species including *E. nigrum* and much moss (NVC H18).
v. *V. myrtillus* heath with a few grasses and sedges and abundant lichens (NVC H19)
vi. *V. myrtillus* heath rich in fescue and lady's mantle (NVC H22).
vii. *E. nigrum* heaths with much *Rhacomitrium* moss (NVC H14).
viii. Sedge-heather moor rich in either mosses or lichens (NVC H9).
ix. *Molinia*-heather moor (NVC H9).

In the Cairngorms *Calluna* is usually dominant and dry heather moorland covers many of the lower slopes of the mountains. The NVC community *Calluna vulgaris-Vaccinium myrtillus* (H12) is particularly widespread. Other dwarf shrubs can be abundant such as crowberry (*E. nigrum*), bell heather (*Erica cinerea*), cowberry (*Vaccinium vitis-idaea*) and bearberry (*Arctostaphylos uva-ursi*). On wetter ground cross-leaved heath, *Erica tetralix*, may be sub-dominant (NVC: M15, M16). Sub-dominance of *A. uva-ursi* can occur in particular in NVC H16 (*C. vulgaris-A. uva-ursi*). This is a relatively rare habitat found chiefly in the Central and Eastern Highlands well known for its richness in bryophytes and lichens. A prime example of this is the Muir of Dinnet NNR[*] (Thompson *et al*. 1995). Common mosses include *Dicranum scoparium*, *Hypnum cupressiforme* and *Polytrichum sp*. Lichens are abundant in many areas of the NNR and in places they form a co-dominant constituent component of the moorland. The main dominants include species of *Cladonia*, of which 28 have been recorded, the most common of which include the bushy species *C. portentosa* and *C. arbuscula* of the sub-group *Cladina*, the goblet shaped *C. fimbriata* and the red tipped *C. floerkiana* (Cairngorms Partnership, Marren 1979, Sanderson 1996). Further information on moorland and upland NVC communities can be found in Rodwell (1991).

The species richness of *Calluna* dominated moorland depends on a number of environmental factors and perhaps most importantly with the time elapsed since the area was last burnt. A number of species are however frequently present: *Genista anglica* (Petty Whin), *Hypericum pulchrum* (Slender St. John's-Wort), *Viola riviniana* (Common Violet), *Carex pilulifera* (Pill Sedge) and *Festuca ovina* (Sheep's fescue). A host of other less

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[*] National Nature Reserve

frequently occurring species are also used as community indicators, some of the most characteristic are listed by Marren (1979).

Associated species of heather moorland include *Carduelis flavirostris* (twite*), Pluvialis apricaria* (golden plover), *Aquila chrysaestos* (golden eagle), *Circus cyaenus* (hen harrier), *Falco columbarius* (merlin) and of course the red grouse (*Lagopus lagopus scoticus*) which is in fact endemic to the British Isles as well as being of economic importance. Red deer and mountain hare are also abundant on heather moorland. A number of rare and threatened insect species are also found in this habitat: the wood ant, *Formica exsecta* is found on open moorland with some trees, while the butterflies *Boloria selene* and *Coenonympha tullia* are found in damp heathland. *Arctostaphylos* heath is important for several species of Lepidoptera (Cairngorms Partnership).

2.3 Lichen diversity on heathlands

In *Calluna* heathlands it should be noted that, in terms of lichens, most are in fact fairly species poor, and frequently only the shade tolerant *Cladonia portenosa* is present. Such heaths are of little conservation interest for their lichen flora and are commonly associated with tall, old heather or with an abundance of grassy species *Deschampsia flexuosa* or in the lowland heaths of SW. England *Agrostis curtisii*. Lichen rich heaths are associated with open canopied *Calluna* stands and much bare ground, with the richest specimens found in heavily grazed areas where the *Calluna* is kept short for many decades. Species rich lichen heaths frequently occur in the transition zone between wet heath (NVC community *Erica tetralix-Sphagnum compactum* M16) and humid heath and through the declining sphagnum cover to the driest heaths such as NVC: *C. vulgaris-Ulex minor* (H2) found in SE. England.

On drier heaths the bushy *Cladonia* species (subgenus *Cladina*) are usually abundant. In species rich heaths *Cladonia portentosa* (= *C. impexa*) is usually frequent and accompanied by *Cladonia ciliata, Cladonia arbuscula, Cladonia uncialis, Coelocaulon aculeatum* and *Cladonia muricatum*. Smaller *Cladonia* species are also common including: *Cladonia cervicornis verticillata, Cladonia chlorophaea, Cladonia coccifera, Cladonia floerkeana, Cladonia glauca, Cladonia gracilis, Cladonia macilenta* and *Cladonia subulata*. Crustose species include *Baeomyces roseus, Icmadophila ericetorum, Trapeliopsis granulosa* and *Placynthiella* ssp. On wetter heaths the cover of bushy *Cladonia* species may decline but others increase in abundance notably *Cladonia crispata, Cladonia strepsilis* and *Pycnothelia papillaria* (Sanderson 1996).

Many of these species are dependant for their survival on the maintenance of an open *Calluna* canopy and relatively low moisture levels as they become rapidly swamped by mosses. There is evidence, which will be discussed later, that lichens in fact have certain mechanisms which allow them to at least slow colonisation by other species and maintain large open patches in which they can thrive. This highlights the misnomer that lichens pave the way for later successional stages, this is probably only true of saxicolous species and the colonisation of bare rock.. In general however the ecology, survival and success of lichen species goes hand in hand with that of *Calluna*, as is the case for many other heathland species. It is necessary therefore to go on to examine the life cycle of *Calluna vulgaris* in detail.

2.4 The *Calluna* Cycle

During its life a plant may pass through several growth phases which can be arbitrarily defined and identified. Watt (1947) proposed four such phases which are perhaps most frequently associated with *Calluna*: pioneer, building, mature and degenerate and stated that a vegetation patch is likely to be greatly influenced by the dominant species passing successively through each of these phases in a cyclical manner. The delimitation of phase is necessarily subjective but is based on visible changes in the morphology and behaviour of the plant. While there is a rough relationship between age and phase this can of course be complicated by environmental factors such as snow, frosting and the nature of the soil and by genetic variations in structure and behaviour (Barclay-Estrup & Gimingham 1969).

The determination of the phases in the life history of *Calluna* have been defined, both by Watt (1947) and Gimingham (1960), and general picture can be drawn up:

- **Pioneer**: the period of establishment and early growth. After roughly 2 years the leading shoot looses its identity and basal branches equal it in height. The plants reach up to15cm in height. Flowering is sparse. The patch is open with a large number of bryophytes and other vascular plants. Depending on circumstances usually the first 3-5 years of growth.
- **Building**: Maximum cover and density of the canopy. Plants reach a maximum of 30-60cm high with thick shoot growth. Flowering is vigorous and the ground stratum below the Calluna is reduced to a minimum. Usually aged 7-15 years.
- **Mature**: Short shoots are more clustered, abundant flowering. A gap may begin to form in the canopy allowing increased light and rising numbers of other plant species particularly bryophytes. Aged roughly 14-25 years.

- **Degenerate**: A well-defined gap forms as the central branches die back. Abundant *Parmelia physodes* on stems. Peripheral branches become flattened. New long shoots are sparse. Rapid increase in other plant species. In theory seedlings of *Calluna* begin to grow in the gap and the cycle begins again with a new plant.

Lichen populations are intrinsically linked to the cycle as it causes great variation in microclimatic conditions. Again however little work has been done that focuses on the role of lichens within this continuum. In their study of vegetational changes in response to the *Calluna* cycle Barclay-Estrup and Gimingham (1969) show how the progressively increasing cover of *Calluna* impacts on other species. Canopy cover was found to reach its maximum late in the building phase. In the mature phase the canopy area remained steady but began to thin out and a gap began to form until in the degenerate phase the canopy was sparse and the gap was well defined with several pioneer seedlings growing in it. The lowest cover values of other vascular plants were found in the building phase and virtually disappeared for a time. While the cover of bryophytes increased during the investigation the number of species actually declined as the damp dark conditions below the canopy favoured *Sphagnum* and mats of a few pleurocarpous mosses. Numbers increased in the degenerate phase however as conditions became more suitable for species favouring more open conditions. At the start of the investigation there was a thriving colony of lichens in the area, canopy closure and competition from mosses meant however that these had virtually disappeared by the end of the study. The general trend in the heathland was towards increasing *Calluna* until the degenerate phase, lowest concentrations of other vascular plants in the building phase becoming re-established in the degenerate phase and reaching maximum cover values as *Calluna* begins its subsequent pioneer phase. The peak of bryophyte diversity was found in areas of degenerate *Calluna* and the same was true for lichens.

Gimingham (1972) summarises the effects of *Calluna* by stating that the prime factor controlling the balance between *Calluna* and other species is the dense shade cast by the canopy. Not only will this effect other vascular plant species such as *E. cinerea, E. tetralix* and *V. myrtillus* which become progressively out grown by *Calluna* and shaded out. This effect is just as valid for lichens however, which become progressively out competed in the dark, damp condition below the canopy in particular by relatively species poor mats of pleurocarpous mosses. Further more he points out that even where *Calluna* bushes are fairly widely spaced the open areas between them may remain bare and lichen covered for many years. He suggests a possible inhibitory effect by a product of *Calluna* roots. This is confirmed by the work of Roff (1964) (ref in Gimingham 1972) who observed the partial suppression of grasses and other angiosperms in a ring around *Calluna* bushes. Interference of mycorrhizal conditions has been put forward by Gimingham (1972) to explain the suppression of tree growth and colonisation in some species in heather moorland.

2.5 Variation over Time and Space of Lichen Diversity

As has already been stated the overwhelming influence in moorland ecology is the life cycle of *Calluna* and the influence it exerts on the microclimate. Thus it is this that which is the key influence on the development of lichen diversity. Barclay-Estrup and Gimingham (1969) suggest that the highest concentration of lichens will be found in the degenerate phase and similarly with bryophytes. Diversity and cover is also suggested to be relatively high in the pioneer phase. Longton (1992) suggests the following general sequence of lichen colonisation. Bare soil, after 1-3 years, Crustose lichens after 3-10 years, Cup lichens after 10-30 years characterised by *Cladonia*. The mosses *Ceratodon purpureus* and *Marchantia polymorpha* as well as *Polytrichum juniperinum*. As has been stated elsewhere closure of the canopy leads to lichens becoming replaced by weft-forming pleurocarpous mosses. Coppins and Coppins (2001) draw attention to the range of lichen habitats on heathland:

- The ground surface (terricolous lichens on mineral and peaty soils and plant debris).
- Small rock outcrops and low boulders (saxicolous lichens mostly shade and damp tolerant species, often intergrading with terricolous species).
- Large boulders and rock outcrops (saxicolous lichens).
- *Calluna* stems (corticolous lichens associated in particular with old and woody stems).

They also draw attention to the existence of some species of bryophilous lichen species which are able to survive in areas where bryophytes are well developed.

It has already been stated that lichen rich patches may persist even in closed canopy conditions. The phenomenon has been studies by Hobbs (1985) and Lawrey (1977). Hobbs carried out experiments to determine in the lab whether they affected plant germination and development through bioassays on seeds of *Avena fatua*, *Calluna* and *Deschampsia flexuosa*. Extracts from podetia were found to have no effect on germination but a significant inhibitory effect on radicle growth on *A. fatua*. Significant reduction in *D. flexuosa* germination was observed and considerable mortality of *Calluna* seedlings also. A field experiment was also carried out where lichen mats were killed off and germination observed. The fact that no germination of *Calluna* took place in treated or untreated quadrats suggests that the physical environment of lichen patches is also unsuitable for germination. Lawrey (1977) explains how the release of lichen chemicals (*O*-methylated depsides and despsidones) also inhibits the germination of bryophyte spores. This is of significant adaptive significance given the degree of niche overlap between lichens and bryophytes on moorlands with them competing for light, nutrients, water and substrate. The fact that bryophytes are generally quicker growing makes this ability all the more important.

In general on moorland we can expect that lichen diversity will be highest in the late pioneer stage while the canopy is still open and in the late mature-degenerate phase when the canopy begins to open up again. Secondary successions following burning are considered more fully in Chapter 3.

2.6 Summary

- Heathlands have a limited range in European terms.
- Heathlands are largely an anthropogenic creation, maintained by burning and grazing, but still of conservation interest.
- The overwhelming influence on vegetation diversities are management techniques and the Calluna cycle.
- Lichens play an integral part in heathland plant communities though their diversity is varied through time and in different areas.

3. MUIRBURNING PRACTICE ON HEATHLANDS

3.0 Introduction

This chapter will highlight the way in which heathlands are managed by muirburning. The areas which will be examined include the practice of muirburning in the UK, variation in the nature of muirburning, the impacts of burning on the physical environment of heathlands and finally guidelines that exist to ensure that burning is carried out appropriately. Having looked at these areas it will then be possible to go on, in Chapter Three, to examine the impacts on heathland ecology.

3.1 The Practice of Muirburning

It was stated in the last chapter that regular burning of large areas of heathland has been common practice in Scotland to provide grazing for a long period of time. For the last two centuries much of the focus has been on burning for grouse management. The traditional system was a rotation of 12 years and to burn small areas to provide a patchwork of habitats. Large areas are however still sometimes burnt for grazing.

Burning practice varies form place to place and also depends on the conditions on the day of burning and the nature of the vegetation. Burning with the wind creates a rapidly moving fire front, burning against the wind creates a slower moving, more intense fire front.

Muirburning normally takes place in the building phase of the *Calluna* cycle to prevent progression to the less nutrient rich, older stages of the cycle and to encourage rapid regrowth to prevent invasion by other species. Burning should be implemented in the autumn to achieve maximum regrowth but is often done in the spring. The aim of management is to achieve a monoculture of Calluna. The quickest regeneration of Calluna occurs by vegetative regeneration from basal buds and is rapid due to a pre-existing root system. Old and moribund plants will however be killed by burning. Fire temperatures are also higher in older stands as there is a higher proportion of dry woody material (Portsmouth University 1999).

Gimingham (1972) identifies the three important points that should control burning:

- Burning should take place in the late building phase to avoid succession to the mature and degenerate phases.
- Fire should consume the majority of above ground material. Temperatures however should not exceed 500 ºC in the canopy and 200 ºC at ground level to avoid compromising regeneration by damaging the plant and setting fire to the peat which could have disastrous consequences.
- Many small fires in long strips are preferable to larger, more extensive ones. It is stated by McVean and Lockie (1969) that the ideal fire size will be 0.4 ha on the basis of the habitat requirements of grouse.

In Scotland burning is restricted to between the 1st October and the 15th April. This is largely to avoid possible negative impacts such as the destruction of nesting birds, fires going out of control and damaging soils. Guidelines for muirburning can be found in the forthcoming SNH* (in press) publication "*The Muirburn Code*" a summary of which can be seen in Appendix 1 (p. 36)

Coppins and Coppins (2001) make the following recommendations for muirburning with regards to lichens:

- Avoid burning close to rock outcrops and large boulders.
- Avoid burning on the sides of steep gullies.
- Avoid burning on sites that are not regularly burnt and are of high conservation value.

While following these guidelines will help to protect lichens in some areas they will be mainly of benefit to saxicolous lichens while others may be wiped out by fire.

3.2 The Nature of Muirburn Fires

i. Temperatures reached in fires

Whittaker (1961) was the first to measure the temperatures reached in moorland fires by using thermocolour paints. She found that at a height of 20cm temperatures ranged between 500ºC and 840ºC. At ground level, even in the hottest fires, temperatures were generally in the range 200-500ºC. The speed of passage of fires was observed to be roughly 1.8m min^{-1} passing over an area in roughly two minutes. Kenworthy (1963) used thermocouples to investigate burn temperatures. The average maximum over 35 fires was

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* Scottish Natural Heritage

found to be 670ºC over 35 fires. Temperatures at ground level however seldom exceeded the range 60-100ºC for periods of thirty seconds or less.

Whittaker emphasised the effects of environmental factors in controlling fire intensity. In particular wind speed and moisture content of the soil and vegetation but also with how the fire is controlled and whether it is burnt with or against the wind. Fire temperature is also controlled by the age of the vegetation when it is burnt. Older stands not only have more fuel but also contain more dry woody material and in the absence of major variations in weather fire temperatures have been shown to increase with age. Temperatures at ground level may be further modified, and stem bases protected by, partial burial in humus, litter and in particular moss mats with those with the highest water content obviously being most effective (Grant 1968).

Fire temperatures are important because they greatly influence the nature of the secondary succession. This will be dealt with in more detail in Chapter 3 but in general the main influences are on the survival of *Calluna* basal stems and seeds and the nature of the substrate left for re-colonisation. Fire temperatures are also of importance as they effect the nature of the substrate that is left behind for re-colonisation. Fires with lower temperatures may just burn off the crown of the vegetation leaving large stems and moss mats near to the ground somewhat scorched but largely intact. This is very different to a hot fire which may remove nearly all of the above ground part of the *Calluna*, burn away mosses below the canopy and scorch the peat surface leaving a dry organic substrate for recolonisation. The nature of the substrate can be expected to have a profound influence on lichen colonisation with drier, open organic sites being much more suitable not least due to the temporary removal of competition from bryophytes, the reverse may of course be true for other plant groups.

ii. Effects of fire on nutrient loss

It is generally accepted that muirburning leads to an overall loss of nutrients from the ecosystem. The losses are somewhat mitigated by input from rain and the weathering of bedrock though to what extent there remain arguments over. In general the loss of nutrients is not a problem as the system is oligotrophic in any case. An increase of nutrients may in fact be more damaging to the community. The immediate effects of fire is that nutrients are either lost through smoke or deposited as ash. Smoke losses for some chemicals are more important than for others, nitrogen readily volatilises for example. An investigation by Thomas and Trinder (1947) showed losses of N increasing steeply at temperatures above 300ºC up to 80% at 800ºC. Elements which form volatile compounds including C, S, and N showed losses of 50% even at lower temperatures. Significant amounts of P, Ca and Mg are also lost depending on temperatures. While some chemicals may condense and be redeposited in the area. Evans and Allen (1971) showed that only a very small amount of the nutrients contained in smoke were returned to the system within 120m of the fire. The remainder of nutrients are deposited on the soil as ash some of which may or may not be soluble and be washed away (Gimingham 1972). In general the result of this is presumably a long-term trend of declining nutrients with short pulses of increased nutrient availability providing a somewhat nutrient enriched substrate for colonisation.

3.3 The Impact of Grazing

The other main management technique on heathlands is grazing. Heathlands are managed both for grazing by sheep and deer and to a lesser impact by grouse and are also grazed by rabbits and hares. Welch (1984) provides a useful summary of grazing on heathlands the ecological impacts of which will be examined more closely in Chapter three. However it is true to say that grazing pressure on heathlands has increased in the last 50 years. This is highlighted by Bardgett *et al.* (1995) who suggest that 38% of heather in Wales and 24% in England showed signs of over grazing. The increase in this pressure can largely be attributed to higher stocking rates of sheep largely as a result of government subsidies aimed at increasing production. In Scotland red deer numbers have also increased. The combination of high grazing pressures and regular burning tends to favour the transition of heather moorland to grassland with associated changes of flora (including lichens), fauna and soils (Sydes & Miller 1988, Welch 1984).

3.4 Summary

- A well-defined set of traditions and directives exist for muirburning.
- Failure to follow directives leads to negative impacts on the moorland community.
- There is great variation in the nature of burns which can lead to a wide range of conditions for recolonisation.
- Burning affects the nutrient status of soils.
- Grazing also plays an important, potentially damaging, part in heathland management.

4. THE IMPACT OF MUIRBURNING ON HEATHLAND ECOLOGY

4.0 Introduction

This chapter will examine how the management techniques described in chapter two impact on the ecology of heathlands. Particular focus will be paid to the impact of muirburning and how this affects lichen diversity. Grazing impacts are important too however and these will also be examined. Chapter one provided an introduction to the ecology of heathlands and importantly introduced the concept of the *Calluna* cycle. As was stated earlier the life cycle of *Calluna* has great impact on the diversity of other accompanying species. Muirburning serves to cut short this cycle and re-initiate it at the pioneer stage. Obviously most other vegetation in the stand will be burned along with the *Calluna*, although due to differences in the nature of the fire (see Chapter 2) this may not always be the case. Following burning secondary succession takes place. The route and length of time this succession takes is largely determined by the time it takes for the *Calluna* to regenerate and re-establish its dominance. This chapter will therefore examine how and why regeneration of *Calluna* varies and the impact this has on other plants, including lichens. It will also examine the direct effect of fire on lichens, the stages of the secondary succession and how lichen diversity and species dominance change over the course of this.

4.1 The Effects of Burning on *Calluna* Regeneration

As has been stated a key influence on the community composition and development of heathlands is the life cycle of *Calluna vulgaris*. It is not surprising therefore that a key influence on the nature of succession following burning is the rapidity with which *Calluna* can re-establish itself. A longer period for colonisation and slower growth will give a better chance for other species, including lichens, to establish themselves at least for a time. It is therefore important to examine what factors affect the speed of re-colonisation and growth of *Calluna*.

i. Vegetative regeneration

Burning destroys the upper part of the plant but in general will leave the lower stems unburnt allowing the *Calluna* plant to regenerate vegetatively from dormant buds lower down on the main stem.

Whittaker (1960 quoted in Gimingham 1972) carried out tests on potted plants which showed that temperatures above 500°C at the stem base for periods of one minute or more were normally lethal. In most fires however temperatures this high are very seldom reached and the basal areas of the stems normally survive. It has been observed however that the ability of plants to regenerate after fire bares a very close relationship to the age of the plant when it was burnt. Gimingham (1972) states that it is generally accepted by most authors that at above about 15 years of age regeneration is either very poor or fails altogether. This may in part be due to the higher temperatures reached when burning older stands but experiments by Kayll and Gimingham (1965) eliminated this effect by cutting away vegetation to a height of 2cm and heating the cut stems with a propane torch. Regeneration was always better in younger and unheated plants.

This simple decline in vigour of regeneration is complicated by the fact that as the stand of *Calluna* ages so stem density declines with a directly proportional decline in sites for vegetative regeneration. This may in fact account for much of the decline in regeneration with age. In chapter two it was stated that regeneration is faster following autumn burning. The reasons for this are unclear but it is suggested that it may be due to new shoots after a spring fire being subject to adverse weather conditions, where as those burnt in autumn would not start to regenerate until after winter avoiding such problems (Gimingham 1972).

ii. Regeneration from seed

Regeneration from seed will usually occur when vegetative regeneration fails due, for instance, to excessive temperatures reached in fires or due to stand age. Regeneration from seed tends to be slower than vegetative regeneration and this is certainly the case when excessive temperatures have been reached as litter and moss mats may have been burnt away taking with them any seeds deposited in them. Regeneration will therefore depend upon seeds in the ground, brought in after the fire or the colonisation of the burn from its edges. Seed and seedling survival are affected by a number of factors. We have already seen for example that lichens produce certain chemicals which may inhibit germination, growth rates and mortality.

The germination of *Calluna* seed is affected by a number of factors. The availability of seed for regeneration should not normally be a problem as *Calluna* seeds retain their viability for a relatively long period of time. Thus seeds found in litter and moss mats will normally germinate following burning. In the case of more extreme fires where litter and even the top 1cm of soil is burnt away seeds buried in the peat for considerable amounts of time will normally still germinate. In addition seeds are easily transported by wind onto the site. In addition a more severe fire may burn away loose litter and moss mats leaving a more, compact seedbed for germination. Hobbs and Gimingham (1987) report that germination rates are lower on beds of pleurocarpous mosses and mineral soils than on organic soils. There is also evidence that the germination of *Calluna* is improved by burning. Results of experimental heat treatments show that while temperatures of 200°C are normally lethal, fluctuating temperatures between 40 and 120°C actually increase rates of germination. In properly managed fires ground level temperatures should not normally exceed this range and even if they do then litter, mosses and the upper soil layers provide insulation meaning only seeds on the surface are killed. In this respect *Calluna* can be seen to be some-what fire adapted especially when one considers that seedlings are hardly ever found under *Calluna* bushes and there is evidence for *Calluna* bushes preventing germination (Gimingham 1972).

Seedling establishment and survival requirements are greater however than those for germination, the critical factor being water availability and protection from desiccation is essential. On a site at Dinnet Moor Gimingham (1972) reports that *Calluna* seedlings were often found aggregated in small hollows filled with mosses where water retention was greater. This despite the earlier reported finding that germination success was lower on moss mats.

Despite how quickly and successfully *Calluna* seedlings manage to establish themselves however, regeneration from seed will frequently be slower than the vegetative method due to the absence of a fully developed root system (Hobbs & Gimingham 1984). When we consider that the speed with which *Calluna* can regenerate is essential for the establishment of other species, and therefore for lichen diversity also, then fires and conditions which encourage slower regeneration are likely to lead to higher lichen diversities.

Having examined the role of fire in the regeneration of *Calluna* it is now possible to go on to examine how heathland vegetation, and in particular lichen diversity develops following burning.

4.2 Secondary Succession Following Burning

There is a great amount of variation in the literature which analyses the regeneration of heathland communities and this disagreement is not just due to the observations of different communities and sub-communities at different times and in different places. Hobbs and Gimingham (1984) draw attention to the problem with many studies of the development of heathland vegetation following burning, namely that they rely on observations of general trends made at one time on many different stands. They draw attention to the fact that many of these stands do not necessarily fit into a developmental sequence and may in-fact be following different developmental pathways. Despite this however it is useful background knowledge to have some sort of broad, generalised sequence upon which one can build their hypotheses. Despite their criticism the first area to be examined is the general development of heathland post-burn, taking into account Hobbs and Gimingham (1984) which tried to overcome these problems by experimental burning and observation of fixed point quadrats.

Ward (1970) showed the successional pathway to be one where lichens are abundant and begin to colonise the bare ground left by the fire after two to three years. Lichens are stated to reach their maximum development after about ten years by which time the ground surface begins to be taken over by faster growing mosses, herbs and shrubs. As the heather canopy closes in the building phase so overall lichen diversity declines as they are replaced by mosses in the damp, darker conditions. Fritsch and Salisbury (1915) however noted that as the canopy closed so lichens such as *C. arbusluca and C. portentosa* increased as did species which use heather stems as a substrate such as *P. physodes.* Some mosses, for example *Polytrichum juniperus* family were observed to colonise rapidly following burning though they were small and sparse. Although these species sometimes go on to form rich mats beneath the heather canopy, particularly on damper moorland this was not observed to be the case at the site studied by Ward (1970) where pleurocarpous mosses were the main benefactors of canopy closure. On drier mineral soils herb species were quick to establish following burning, possibly at the expense of lichens, these however were once again quickly replaced by mosses following canopy closure.

The experimental study of Hobbs and Gimingham (1984) however draws attention to the problems they warned of as there is considerable variation in the development of the communities. This is largely attributed to the age and development of the stand at the time of burning. Regrowth of the main Ericaceous species was observed to be most rapid in areas which were pioneer or building phase when burnt. In older stands species such as *V. myrtillus* were able to attain dominance where regeneration was slower. Grass and forb species re-appeared abundantly only in those stands in which they had been abundant before although the number of species present does not seem to be entirely linked to their presence before the fire. Frequencies of these species declined in the building phase only to increase in the mature–degenerate phases and with them centres for vegetative regrowth. The fact the soil seed bank may become depleted as the stand ages (Mallik *et al.* 1984) explains these trends somewhat. It is suggested that differences immediately after the fire may persist for some time. Grasses forbs and lichens however seem better able to recolonise where they were initially absent. Pleurocarpous mosses may colonise rapidly following burning growing from the centre of old mats. These species are normally only present following the closure of the *Calluna* canopy and may pose a significant barrier to colonisation by lichens and vascular plants. The study of Hobbs and Gimingham (1984) suggests that the initial floristic composition is key to determining the developmental pathway the site will take following burning and is something that needs to be carefully considered when considering the succession of heathlands.

In summary there are number of controls on the post-fire succession of heathlands not least determined by the pre-fire nature of the stand. Ratcliffe (1959) points out that key controlling factors in vegetation development are the gradient of soil wetness, the gradient of soil base status and the gradient of anthropogenic influence thus environmental conditions and human management may have just as great an effect on post-burn development as the initial floristic composition. This latter control seems common sense really but perhaps its greatest effect is on the more species rich moors where various species are available to colonise an area. On poorer heaths while the nature of the stand may influence the rate of regeneration of heather cover and the nature of the vegetation immediately following the fire in the absence of extreme conditions the re-establishment of *Calluna* dominance and the influence of the *Calluna* cycle seems assured.

4.3 Lichen Succession on Heathlands

Having considered the general nature of succession on moorlands it is now necessary to examine how lichen diversity and species composition varies over time as well as to examine the reasons for these changes. After a brief examination of the impacts of mismanagement it should then be possible to draw some general conclusions about the impact of muirburning on lichen diversity.

The concept of initial floristic composition certainly has some role to play when considering the post-burn development of lichen populations. Recolonisation of an area will be greatly speeded up if stands contained a number of species to begin with and a number of individuals survive the fire. *Cladonia* species can survive cool fires and fifty percent or more of the lichens may survive if there is not much litter to retain the fire (USDA). This may be the case at the edge of the burn where temperatures are lower, in generally low temperature fires and where they are protected by hollows, litter or mosses. Examples of differing lichen "tolerances" have been compiled by Coppins and Coppins (2001) and can be seen in Appendix 2 (p. 37). These values do not represent true tolerance but are a reflection of the speed of reproduction and colonisation or of the lichens ability to avoid burning by having a significant proportion of their individuals in protected areas, e.g. in wet patches where burning is incomplete.

Conditions following a fire are often very different to those beforehand (Mallik 1986) and thus present an opportunity for colonisation of the stand by lichens where previously mosses and shrubs dominated. Longan and Gomez-Bolea (1998) suggest that for epiphytic lichens a burnt substratum may actually favour the establishment of some species and this may be equally true for terricolous colonizing burnt or scorched peat. In the case of terricolous species on heathland burning certainly creates conditions more amenable to lichen diversity if not directly encouraging it. Gimingham (1972) suggests that the post-fire nature of lichen heaths makes lichen richness possible due to the more open conditions. On lichen rich heaths diversity is normally due to a low irregular canopy which is approximated in the young pioneer *Calluna*. While Fos *et al.* (in press) suggest that the lichen species colonising a newly burnt site will be those with the greatest ecological amplitude this is not obvious due to the relative lack of information about the conditions favoured by lichen species. What is clear however is that there is a general trend in the development of lichen diversity and there is a great difference in their alpha and beta diversity with the diversity over time and the course of the community succession and the *Calluna* cycle much greater than that at any one time. The view of Hobbs and Gimingham (1987) was that the development of lichens following burning was generally as follows:

Lichen Succession: *Lecidea granulosa*, *L. uliginosa* ⇒ *Cladonia* spp.

Ward (1970 p.854) states that *Cladonia chlorophaea*, *C. coccifera*, *C. coniocraea*, *C. crispata*, *C. fimbriata*, *C. floerkeana*, *C. glauca*, *C. pityrea*, *C. subulata* and *C. uncialis* are species which colonise the bare humus after burning. Cladonia *portentosa* and *Parmelia physodes* grow under a mature or degenerate canopy, *C. gracilis* and *C. squamosa* are also capable of surviving/colonising under the *Calluna* canopy. Hobbs and Gimingham (1984) drew attention to the importance of initial floristic composition and FIRE EFFECTS and Coppins and Coppins (2001) to the survival of lichens during heathland fires which raises the possibility that species normally associated with closed conditions may be present following burning. The data of Coppins and Coppins (2001) suggest that the species most likely to be present immediately following burning are likely to include: *Baeomyces rufus*, *Cladonia chlorophaea*, *C. diversa*, *C. fimbriata*, *C. floerkeana*, *C. furcata*, *C. macilenta*, *C. polydactyla*, *C. squamosa*, *C. subulata*, *Omphalina ericetorum*, *Placynthiella icmalea*, *P. oligotropha*, *P. uliginosa*, *Trapeliopsis granulosa* (for a full listing of fire tolerance see Appendix 2, p.37). The ability of lichens to colonise an area may be further enhanced by conditions following burning, Southorn (1977) suggests that high pH, soluble organic substances and high concentrations of macro-nutrients may depress bryophyte growth in the first 18 months following burning giving lichens a chance to "get their foot in the door."

The main control on the continued presence of lichens is that nature of the *Calluna* canopy. As the canopy changes and the nature of the near-ground micro-climate changes to darker moister conditions (Mallik 1986) so lichens become replaced by moss species such as *Hypnum cupressiforme*, *Hylocomium splendens* and *Pleurozium schreberi*. The declining diversity as the stand ages is somewhat made up for however through colonisation by species such as *C. portentosa*, *C. arbuscula*, *P. physodes*, *C. squamosa* and *Cladonia crispata* which are adapted to conditions in the closed *Calluna* canopy. The colonisation of large older stems by epiphytic lichens means that while α[1] lichen diversity may decline as terricolous species are swamped by pleurocarpous mosses β diversity[2] is much higher. On top of this lichen diversity in an area may remain high due to the persistence of open lichen

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[1] Diversity at any one point in time.

[2] The diversity of all species throughout temporal changes.

rich patches. The patchwork of young an old heather on a traditionally, well-managed moorland is therefore favourable for lichen diversity.

4.4 The Impacts of Mismanagement

McVean (1959) stated that muirburning had caused the following deterioration's in soils and vegetation:

- Increasing bare, lichen-crusted patches among the heather.
- An increasing extent of bare boulders, stones and rock outcrops showing on hillsides.
- The appearance of bare, soft peat eroded by sheet wash and gullying.
- Appearance of deep gullies on steep heather slopes where peat overlies glacial sands and gravels.
- Hagging of deep peat.

Despite these observations if management is carries out properly and with due care then these issues do not necessarily arise, indeed the first point is something of a plus in the context of this study suggesting that lichens benefit somewhat from muirburn. It is necessary therefore to consider the risks of mismanagement and the impacts it has on heathland and lichen ecology.

i. The impact of grazing pressure

Grazing is the other main management tool on heathlands and has not really been considered in the course of this study. Light grazing has little negative effect on heathland ecology. Grant (1968) noted that sheep and other grazing animals tended to congregate on newly burnt sites grazing these in preference to older areas. Younger *Calluna* has a higher nutrient content than older, more woody plants while grass and forb species such as *D. flexuosa* may germinate following burning. These are usually preferred by sheep and deer and will be removed in preference actually favouring the regrowth of *Calluna*. Welch (1984) reports that light grazing favoured ericoids and lichens e.g. *C. portentosa*, *E. cinerea*, *E. tetralix* and *P. physodes* as well as *Calluna*, particularly on moss rich heaths. *Nardus stricta* and *V. myrtillus* were favoured by intermediate levels of grazing and it has documented that *V. myrtillus* can achieve dominance over *Calluna* where grazing is at the right level. Heavy grazing however greatly favours graminoid and forb species e.g. *Agrostis tenuis*, *Anthoxanthum odoratum*, *Festuca ovina*, *Poa pratensis*, *Rumex ecetosella* and *Trifolium repens*. Grant suggests that this effect is compounded where the burnt stand was older as regeneration is from seed and seedlings may become rapidly uprooted. Heavy grazing, which is common in a number of areas due to high stocking rates encouraged by subsidies, is acknowledged therefore to encourage the transition of heathland to upland grassland. Heavy grazing also encourages the spread of pest species some of which, for example *Pteridium aquilinum*, may be difficult to remove once they become established. Such trends have been documented by Sydes and Miller (1988), Thompson *et al.* (1995) and Welch (1984). Viney (1996) relates the tale of whole hillsides being reduced to black sludge with little or no vegetation due to the effects of over-grazing. The reliance of lichens on the differing conditions of managed heather moorland for their diversity means that any transition to grassland is likely to impact severely on their diversity.

ii. The impact of mismanaged fires.

Any burning of heather needs to be carefully carried out to prevent needless harm to the ecosystem. In the west of Scotland large areas of heather are often still burnt in the belief that it improves grazing for sheep and deer. In the wetter conditions of the west burning will in general encourage the growth of less palatable species such as *Nardus stricta* and *Trichophorum cespitosum*. Circumstances that may lead to delayed regeneration, such as poor weather conditions leading to hot fires and the burning of *Calluna* older that 15 years, should be avoided. The problems facing many of the estates and hill farmers today means however that there is often insufficient time and manpower to ensure proper management. The results can include increased surface run-off and peat erosion as well as poor regeneration and competitive vigour of *Calluna* (Gimingham 1972).

Occasionally fires can get completely out of control meaning excessive areas are burnt and on occasion the underlying humus may even be ignited which can have disastrous effects burning large areas down to the sub-soil and the fire spreading underground killing large areas of vegetation. Radley (1965) and Bayfield *et al.* (1984) showed the difficulty with which vascular plants have in colonising exposed sub-soils following a severe burn. In many cases regeneration is very slow and may be limited to lichens and bryophytes for many years.

4.5 Summary

- Regeneration of Calluna following burning is the key element in heathland succession.

- The succession can take a number pathways depending upon the rate of Calluna regeneration.
- Lichens have a complex succession of their own and their diversity and species changes over the course of the heathlands regrowth.
- Poor management can lead to long-term changes in moorland ecology.

5. DISCUSSION

This literature review has examined the areas that affect lichen diversity on heathlands and given an idea of how heathland management, in particular muirburning, affects this diversity.

The controlling factor in heathland ecology is the life cycle of Calluna. This cycle is somewhat interrupted by the process of muirburning which intends to maintain Calluna in the pioneer to building phases, usually in a patchwork of small burnt areas corresponding largely to the requirements of grouse. Burnt areas of exposed peat provide an ideal substrate for colonisation by lichens. Calluna influences other species around it by the microclimate it creates, outgrowing other shrub plants and shading them out creating moist dark conditions below its canopy generally unsuitable for lichens but an ideal habit for the formation of wefts of pleurocarpous mosses.

There is much argument about the rights and wrongs and this paper has touched on some of those issues. Muirburning prevents the regeneration of woodland and scrub and can lead to high erosion rates and permanent ecological damage. Some people might be tempted to see the very existence of moorlands as evidence of this. Heathlands are however important communities in their own right with a significant history and value both in an ecological and an environmental sense.

In conclusion the issue of muirburning is a complex one and certainly there is much to be said for allowing the regeneration of woodlands but this should be done without loosing sight of the importance of heathlands and their place in the range of habitats present in the British Isles. With regard to lichens this paper has shown how moorland ecology and management impacts on their diversity and abundance. There is a range of lichen species from those that favour the open conditions following fire to corticolous species that develop on heather stems after a ten to twenty years. It has shown that while lichens do not benefit directly from burning, normally being destroyed by the fire, the patchwork of young and old heather and bare peat created by muirburning allows a greater number of lichen and bryophyte species than would be the case in a stand of degenerate or mixed age heather. The open spaces created by burning being crucial to lichen establishment.

Sanderson (1996) summarises this all nicely by stating that there are three factoids[*] commonly thrown around about moorland management and lichens:

- Grazing damages lichen communities.
- Fire damages lichen communities.
- Only mature and degenerate heaths are lichen rich.

While the first two may be true where they are used irresponsibly they in actual fact can help to encourage diversity. The third statement if just untrue however. It is however important to bear in mind guidelines about muirburning and in reference to lichens particularly those of Coppins and Coppins (2001)who suggest it is sensible to avoid burning near gullies to prevent erosion and near rock out crops and large boulders to avoid damage to slow growing saxicolous lichens.

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[*] See Rackham (1990) for a definition.

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APPENDIX 1

A Summary of Muirburning Guidelines

- Identify fire free areas: Summits and exposed ridges, steep hillsides and gullies, where soil is very thin or eroding, blanket bogs and bogs on deep peat, peat haggs and areas of exposed peat, areas where bracken is present, in mixed age stands, woodland, woodland edges and scrub.
- Identify areas where burning will be beneficial.
- Determine the amount of burning to be done and the size of fires.
- Ensure effective firebreaks.
- Make sure fire control equipment is ready.
- Consult with neighbours and management partners (*e.g*. SNH, Historic Scotland).
- Burn only when weather is suitable.
- Light and control fires carefully.

More information is available in *The New Muirburn Code* (SNH in press).

APPENDIX 2

"Tolerances" to Burning of Various Lichen Species

From: Coppins and Coppins (2001).

+	rapidly colonising after burning, within 5 years
++	moderately tolerant
+++	intolerant
++++	not recolonising for at least 20 years

e	Often on *Calluna* stems (corticolous).
w	Tolerant of wet conditions where worst effects of burning may be avoided.

Species in **bold** type are Nationally rare or Nationally scarce.

Absconditella sphagnorum	+++	w
Baeomyces placophyllus	++	
B. rufus	+	
Bryoria fuscescens	++++	e
Cetraria islandica	++++	
Cladonia arbuscula	++++	
C. bellidiflora	++++	
C. carneola	++++	
C. cervicornis	++++	
C. chlorophaea agg.	++	
C. ciliata s.lat.	+++	
C. cornuta	++++	
C. crispata	+++	
C. diversa	+	
C. fimbriata	++	
C. floerkeana	+	
C. furcata	++	
C. glauca	+++	
C. gracilis	++++	
C. incrassata	+++	
C. macilenta	+	
C. mitis	++++	
C. peziziformis	+	
C. phyllophora	++++	
C. polydactyla	++	
C. portentosa	+++	
C. ramulosa	+++	

C. rangiferina	++++	
C. scabriuscula	++++	
C. squamosa s.lat.	++	w
C. strepsilis	+++	w
C. subulata	++	
C. sulphurina	+++	
C. uncialis s.lat.	+++	w
Coelocaulon aculeatum	++++	
Hypogymnia physodes	+++	e
Icmadophila ericetorum	+++	
Micarea leprosula	+++	
M. melaena	++	
M. lignaria	+++	
Omphalina ericetorum	+	
O. hudsoniana	+++	
O. luteovitellina	+++	
Parmelia spp.	+++	e
Peltigera didactyla	+	
P. lactucifolia	+++	
P. membranacea	+++	
Placynthiella icmalea	+	
P. oligotropha	+	
P. uliginosa	+	
Platismatia glauca	++++	e
Pseudevernia furfuracea	+++	e
Pycnothelia papillaria	+++	w
Sphaerophorus globosus	++++	
Trapeliopsis flexuosa	+	e
T. glaucolepidea	++++	
T. granulosa	+	
T. pseudogranulosa	++	
Usnea spp.	++++	e

PRACTICAL PAPER

ABSTRACT

An investigation of muirburning was carried out at Mar Lodge Estate, Braemar with the intention of quantifying changes in lichen diversity as a result of muirburning and the subsequent regeneration of the vegetation. Following consultation with the estate ecologist and head stalker two areas were chosen for research representing two different NVC communities and the presence and absence of grazing. Each area was mapped recording individual burns. 100 quadrats were carried out, 2 in each of 37 burns representing stands from 4 months old to 18 years. 26 unburnt sites were also sampled. Environmental data was recorded for each quadrat as were the species and their dominance for vascular plants, bryophytes and lichens. The data collected was compiled into spreadsheets prior to analysis. This was carried out using a variety of computer programmes including Microsoft Excel, Minitab and PC-Ord. There was an immediately obvious distinction between Areas 1 and 2 due largely to the differences in their underlying environmental conditions. Several analysis confirmed this including a GLM which gave area a T-value of 4.34. Regression analyses were carried out both including and excluding data from unburnt sites which for Area 1 produced regression curves for the graphs plotting lichen diversity against time since burning. This showed lichen diversity increased up to 12-15 years following burning but declined thereafter probably due to the influence of the *Calluna* micro-climate. As well as this a predictive equation was created via a stepwise regression. Soil moisture emerged as the principle significant covariant although the first stepwise regression also showed the age of the stand at the time of burning to be significant. DCA analysis created ordination graphs which highlighted the difference between the two different area and confirmed the link between the time since fire and lichen diversity as well as showing the similarity in composition between quadrats of similar age and soil moisture. "Ellenberg" numbers produced by Dr. C. Legg linked changes in vegetation to changing N concentration and pH following burning.

1. INTRODUCTION

This project aims to quantify the impact of muirburning on lichen diversity. The project was carried was carried out at the Mar Lodge Estate between the 16th and 29th of July 2001. The estate is located five miles to the west of Braemar and is owned by the National Trust for Scotland (NTS). The estate covers 77,500 acres of which around 23% is in the Cairngorms National Nature Reserve (NNR). The area includes large areas of heather moorland, remnants of Caledonian pine forest in Glens Lui, Derry, Luibeg and Quoich as well as mires, grasslands, lochs and montane habitats. The estate lies within a special protection area and in the National Scenic Areas of the Cairngorm Mountains as well as within the boundaries of the proposed Cairngorms National Park. There are also two Ramsar sites within the estate. The landscape is mountainous and heavily influenced by the impacts of glaciation. Roughly one quarter of the estate lies between 300 and 1300 metres above sea level, including 14 Munroes[*]. The soils are largely thin, stony infertile and acidic being derived from the breakdown of the bedrock and glacial deposits. In many areas mineral soils are overlain by extensive peat deposits, particularly where bogs have developed in valley bottoms and under the plagioclimax communities of heathland (EEE website).

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[*] A mountain over 914m

The management Plan of the NTS has presented the estate with several conflicting interests including management for sporting and hunting to maintain the estates traditional and economic value, management to encourage the regeneration of native forests, scrub and woodlands and management for recreation and education. The specific management aims and objectives of the Trust can be seen at the EEE website. The Trust state in their Initial Management Plan:

> "The principle and overriding aim is to manage the land in a sustainable manner, for the benefit of the nation, ensuring the continuing conservation and restoration of its internationally important flora, fauna, wild-land quality and archaeological value… To ensure appropriate public access to the land subject to the maintenance of the landscape and nature conservation interests… To aim to manage the land in a way that enhances the social economic and cultural well-being of the local community."

In heathland areas the response of the Trust has been to attempt to cease muir-burning in some areas and to lower grazing pressure both by excluding deer from some areas and ceasing winter feeding to bring the population down. The current population of deer is about 3,000. There are no sheep grazed on the estate. In the context of this study Area 1 is still both grazed and burned while in area 2 grazing has been excluded (except by grouse) and it has not been burned for around 6 years. These management changes have created obvious tension between the game keepers, many have worked on the estate for many years under several owners and are finding themselves having to radically adjust their practice, and the estate managers who sometimes display the common prejudices against muirburning and grazing.

While much literature has been published on the heathland ecology, perhaps largely as a result of the influence of sporting and agriculture interests much of this has focused on the ecology of and influence of *Calluna* and with scant attention to other groups of heathland species. As the previous paper showed, lichens play an important part in the ecology of heathlands and heathlands are an important habitat for many lichen species. In general the traditional management of *Calluna* combined with the maintenance of some older areas of heather can lead to high lichen diversity. This trend has not however been studied in much detail with many observations limited to passing observations in more general papers. There is therefore a need for better understanding of the nature of lichen communities on heathlands if we are ever to understand the overall importance of this habitat. In the presence of changes in management practice as were described earlier it is perhaps even more essential that we understand the relationship between lichens and muirburning if they are to be protected.

The previous paper described the nature of moorland ecology, management and the impacts muir-burning has on heathlands and on lichen diversity. It introduced the concept of the *Calluna* cycle and the nature of secondary successions of heathland following burning as well as the changing species make up and diversity of lichens. Importantly it also described the history of moorlands and explained their importance and the place traditional management has to play in maintaining their importance. Having examined these issues there now exists a clear backdrop of information on which to base the investigation and interpretation of the impact of muirburning on lichen diversity. From the information that exists on the role of lichens in heathlands communities we can expect that burning will lead to a decline in diversity as they will largely be destroyed by fire. The period following burning will lead to open conditions and, where moss mats have been burnt away, bare peat suitable for colonisation by lichens. The period following burning will therefore see an increase in diversity before the closure of the *Calluna* canopy creates dark damp conditions favouring mosses over lichens.

2. OBJECTIVES

This paper had a number of objectives:

- To identify, in consultation with the stalkers and estate management, areas suitable for the study.
- To map and age the burns in the selected areas.
- To sample the burns and a number of unburnt areas recording all relevant data (see methodology).
- To analyse the recorded data and examining the relationship between the time since burning and lichen diversity taking into account all relevant covariants.
- To produce, through regression analysis, an equation to predict lichen diversity in heathland communities.
- To carry out a Detrended Correspondence Analysis (DCA) to explain the differences in lichen diversity between quadrats.

- To produce a series of Ellenberg numbers capable of explaining changing lichen diversity in relation to their environmental preferences and changing conditions following burning.

3. HYPOTHESES

The background information provided by the literature review allows the formation of a number of hypotheses:

1) Lichen diversity will be low following burning.
2) Diversity will increase with time since fire.
3) Diversity will decline from the building phase.
4) Species present will alter with corticolous species becoming more common as stand age increases.
5) Changing diversity will be linked to changes in the microenvironment caused by burning and post-burn vegetation development.

4. METHODOLOGY

Consultation was carried out with Kate Proctor the estate ecologist and the head stalker. Sampling areas were limited by stalking activities in the high glens and concern about disturbing grouse on the higher slopes due to low numbers and a short time to the start of the season. Two areas were selected. Interviews and site visits with the head stalker provided evidence for the age of the majority of fires and anecdotal evidence about their nature. Evidence from these discussions was confirmed by observation on the ground. The interview also provided information on grazing pressures and estate policy in the two areas. Site visits were carried out with Kate Proctor to aid in the determination of NVC[*] communities and with vascular plant identification.

Mapping and sampling of Area 1 was completed in the first week, Area 2 was completed in the second. Mapping of the burns was carried out in the field. Burns were photographed and mapped onto a 1:10,000 scale maps and numbered. Maps and photographs can be in Appendix 1 (p. 71).

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[*] National Vegetation Classification

As variation in burn conditions and post-fire vegetation development is likely to be greatest between different fires rather than over individual burns sampling strategy aimed to include the great variation that can occur between different burns. For this reason emphasis was placed on sampling the maximum number of burns possible with a reduced number of quadrats in each. Burns that gave the maximum possible spread of ages were selected for sampling. Two quadrats were completed in each burn selected. Greig-Smith (1983) states that the value of quantitative data on the composition of vegetation depends on sampling procedure. As Greig-Smith points out the random placing of a quadrat is not as simple as throwing it over one's shoulder. The simplest method of randomisation involves putting down a grid and selecting random numbers as co-ordinates. Such a strategy was not however practical in this situation. The method chosen therefore was based upon Stratified Random Sampling described by Smartt and Grainger (1974). Each burn was divided horizontally in half with one sampling point being located in each strata according to the burn number which determined the vertical distance and the quadrat number which determined the horizontal distance. If the distance led to a position beyond the edge/boundary then the remaining distance was re-bounded back. While it is acknowledged that this will have led to some bias towards the edges in the early quadrats this was preferable given the drawbacks of other techniques which involved the placing of a grid and other techniques such as the random walk. This is especially true given the difficulty involved in generating random numbers in the field. Unburnt points were placed as systematically as possible (the density of burns made this difficult in some areas) with one quadrat carried out at each point. In all 100 quadrats were carried out, 70 in area one and 30 in area two. 38 burns were sampled, with two quadrats in each, and 24 unburnt points. Samples were completed using a 1 m^2 quadrat. Quadrats 1-69 are located in area one and 70-100 in area two. Maps of the areas investigated showing the location of burns and of unburnt quadrats can be found in Appendix 1 (p. 71).

For each point the following information was recorded: quadrat number, burn number, altitude, aspect, slope, soil type and moisture, time since fire, fire intensity (which was estimated from unburnt stems), age and stage of vegetation when burnt (estimated by looking at vegetation surrounding the burn, the current stage and height of the *Calluna*, prominent local features, NVC category. Also recorded were vascular plant species, mosses, lichens and their cover values. Arbitrary five point scales were used for cover values, slope, soil moisture and fire intensity and these can be seen in Appendix 2 (p.77).

Identification of vascular plants was largely carried out in the field. A number were sampled in the field and identified later using McClintock and Fitter (1974) and Mabey (1996). Bryophytes were identified in the field, a number were sampled and identified later using the following keys: Hill (1992), Jahns (1983), Watson (1978) and a reference collection created by Kate Proctor. 19 samples were identified by David Long at the Royal Botanic Gardens Edinburgh. Lichens were largely sampled in the field and identified in the lab by the author using a microscope, hand lens and the following keys: Dobson (1992) and Hodgetts (1992). The following tests cause colour changes in some lichen species and were carried out in order to aid with identification:

- K = potassium hydroxide
- C = calcium hypochlorite
- K + C = K is applied to the specimen and taken up on filter paper. A drop of C is placed next to it and the colour change observed where they meet.
- C + K = the opposite procedure to that above.
- P = paraphenylenediamine crystals wetted with alcohol and the liquid applied to the specimen.

19 samples, which proved difficult to identify, were sent to the Royal Botanic Garden Edinburgh and identified by Brian Coppins.

Raw data from the quadrats were compiled into to tables in Microsoft Excel. Analysis of the data was carried out in Microsoft Excel, Minitab. PC-ORD was used for the DCA analysis. Further explanation of the analyses carried out can be seen in Section 5. Ellenberg numbers for species and quadrats were prepared by Colin Legg and was analysed by the author using Minitab. The raw data can be seen in Appendix 3 (p. 78).

5. RESULTS

This section aims to simply present the results of the investigation and provide a brief explanation from some of the trends. Detailed analysis and explanation of the results will be dealt with in the following section. Raw data tables showing the information collected in each quadrat can be seen in Appendix 3. Before presenting the details of the analysis a number of general points: 45 species of lichen were recorded in total including 31 terricolous, 11 corticolous and 3 saxicolous. A total of 22 *Cladonia* species were identified which compares favourably with the famously Lichen rich Muir of Dinnet NNR where 28 species of *Cladonia* have been identified (Marren 1979).

5.1 Differences Between Areas One and Two

i. Differences in the physical environment and lichen diversity

The raw data have showed that there is significant difference between the results from area one and area two. In terms of the vascular plants area one is dominated by NVC community H12 with *Calluna vulgaris* dominant and *Vaccinium myrtillus* and *Vaccinium vitis-idaea* sub-dominant. There is also an area of *C. vulgaris-A. uva-ursi*, (H16) which is usually associated with high lichen diversity, on the south facing slopes at the far end of area one. Area 2 on the other hand largely consists of community H10 again dominated by *C. vulgaris* but with *Erica cineraea* sub-dominant with *V. myrtillus* subdominant in places. The graphs that can be seen in Appendix 4 (p. 87) show that the environments of Areas 1 and 2 also appear to be significantly different with, on average, shallower slopes, drier and stonier soils, a lower range of altitudes more southerly facing slopes.

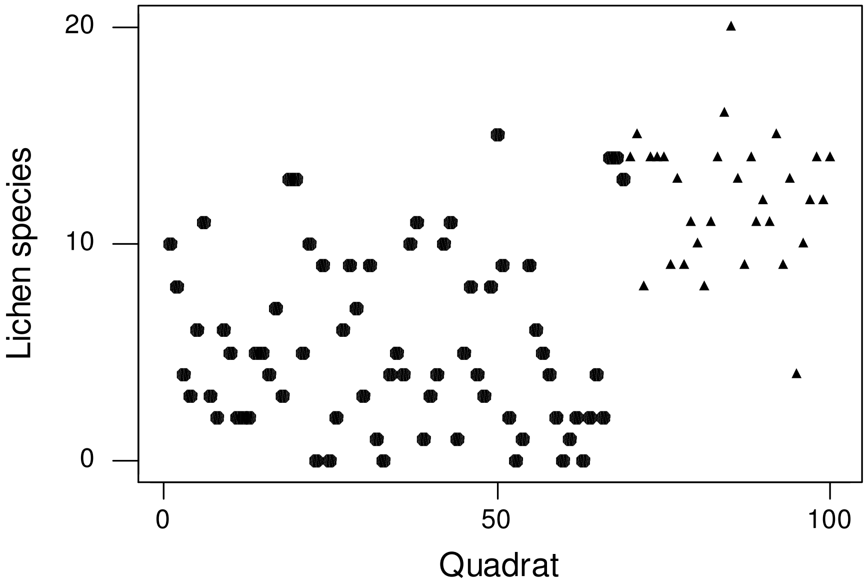

Fig. 1. Lichen diversity in Areas 1 and 2. • = Area 1 ▲ = Area 2

As can be seen from Figure 1 and Appendix 4 the diversity of mosses and lichens are on average also different between the two areas. Area one has on average more mosses and significantly less lichen species than area two. These differences are linked to the differing conditions at the two sites. The drier conditions have led to a much thinner canopy of *Calluna* and explain the co-dominance of *E. cineraea* (Gimingham 1972). This scenario has created a significantly different microclimate in the two areas and the drier more open conditions in Area 2 have favoured lichens over mosses and they have effectively filled this niche. The significance of the differences between the two areas makes it necessary to examine them separately. Unfortunately this meant that little analysis was possible on the data from area two as there were no burns younger than 6.5 years. This also impacted on the data as a whole as the majority of these middle-aged burns were located in area two. However some analysis (below and in Section 5.4) has been carried out on the data as a whole however and this shows the importance of the difference between the two areas.

ii. General Linear Model

A General Linear Model (GLM) was run using Minitab to investigate the significance of the differences between areas one and two. The GLM modelled the difference between areas one and two using altitude, aspect, slope, soil moisture, time since fire, fire intensity, stage when burnt and the current stage as co-variables. Quadrant number was also included as a covariant in order to determine the possibility of bias in the data. Of particular concern was the possibility that due to improving skills of identification more/different species were recorded in later quadrats compared to earlier ones. The full GLM print-out can be seen in Appendix 5 (p. 88). The model shows the importance of area in determining lichen diversity with a high coefficient of 6.798, a P value of 0.000 and a T value of 4.34. The GLM also shows the importance of the time since burning which also has a T value of 3.74 and a P value of 0.000. Soil moisture also has significant influence with a P value of 0.007, a T value of –2.79. Quadrat number also appears as fairly a significant influence on diversity with T and P values of –2.38 and 0.020 respectively. The model therefore highlights the importance of the difference between the two areas suggesting the need for separate analysis. It also provides introductory evidence that burning does indeed have a significant impact on lichen diversity while soil moisture also acts as an important control.

5.2 The Relationship Between Time Since Burning and Lichen Diversity

i. Time since burning versus diversity

These graphs plot lichen diversity against time since fire for each quadrat. Areas 1 and 2 are plotted separately. Unburnt quadrats are included for comparison purposes with an arbitrary value of 25 on the x axis. The graphs for lichen species diversity in areas one and two can be seen above and below (Figures 2 and 3 respectively).

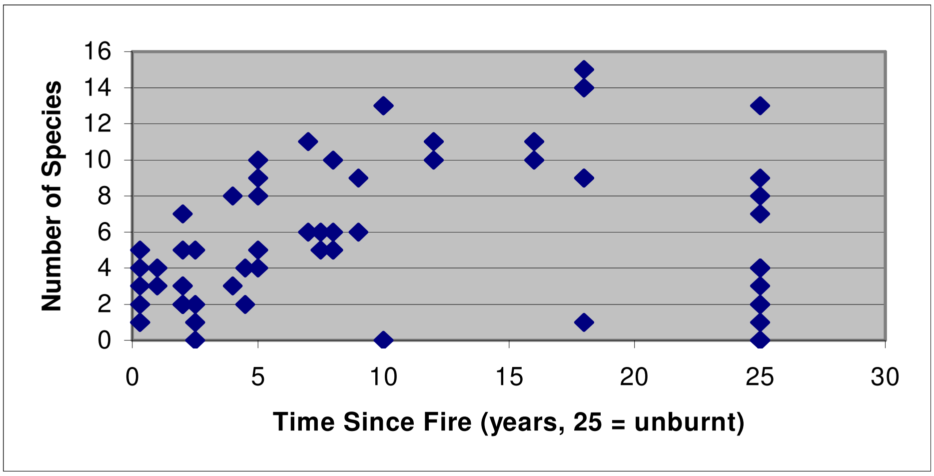

Fig. 2 Change in lichen diversity with time since burning in Area 1

The graph for Area 1 shows increasing species diversity with time since burning followed by a slight decline after 10+ years. Unburnt quadrats show a large amount of variation in their diversity but in general diversity is lower. This is somewhat masked by the fact that several points are plotted on top of each other and can be more clearly seen in Section 5.3. No clear trend can be seen from the graph of Area 2 as this area has not been burnt for at least six years. However a slight increasing trend can be seen while diversity is again lower in unburnt stands. The clarity of the results have been affected by dealing with each area separately. There are no results in Area 2 for any burns older younger than six years. The fact that burning was concentrated in this area from 6 years ago may explain the lack of data in Area 1 for burns aged 10-15 years.

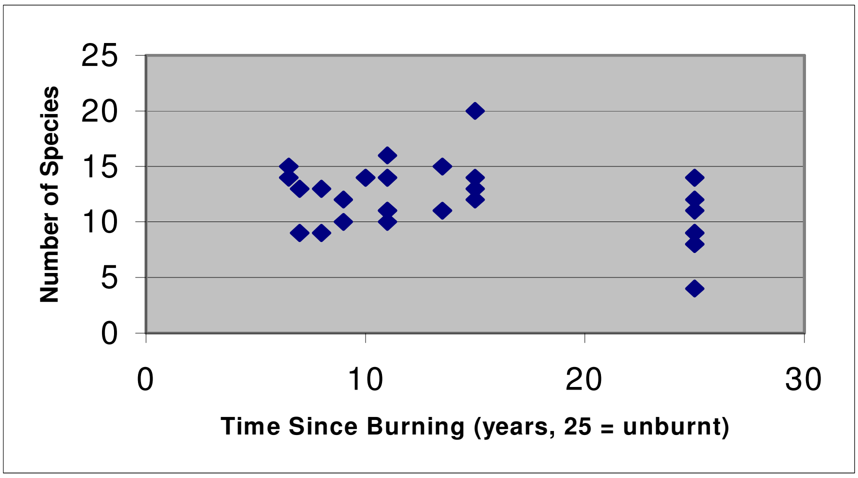

Fig. 3. Change in lichen diversity with time since burning in Area 2.

A graph was also plotted to show changes in bryophyte and vascular plant diversity following burning in Area 1. These can be seen in Appendix 6 (p. 91). The results are not so clear as those for lichen species. There does however appear to be a fairly rapid increase in diversity during the first 5 years following burning followed by a slight decrease from ten years onwards. Once again the graph is less clear due to the absence of data for middle-aged stands.

ii. Polynomial regression

In order to fit a curve to these graphs a polynomial regression was carried out using Minitab. The missing data meant that this was unfortunately impossible for the data from Area 2. Two graphs were plotted: one excluding data for the unburnt stands (Figure 4) and one including the unburnt stands giving them an arbitrary age of 25 (Figure 5). The fitted line graphs can be seen below as well as the equations they produced.

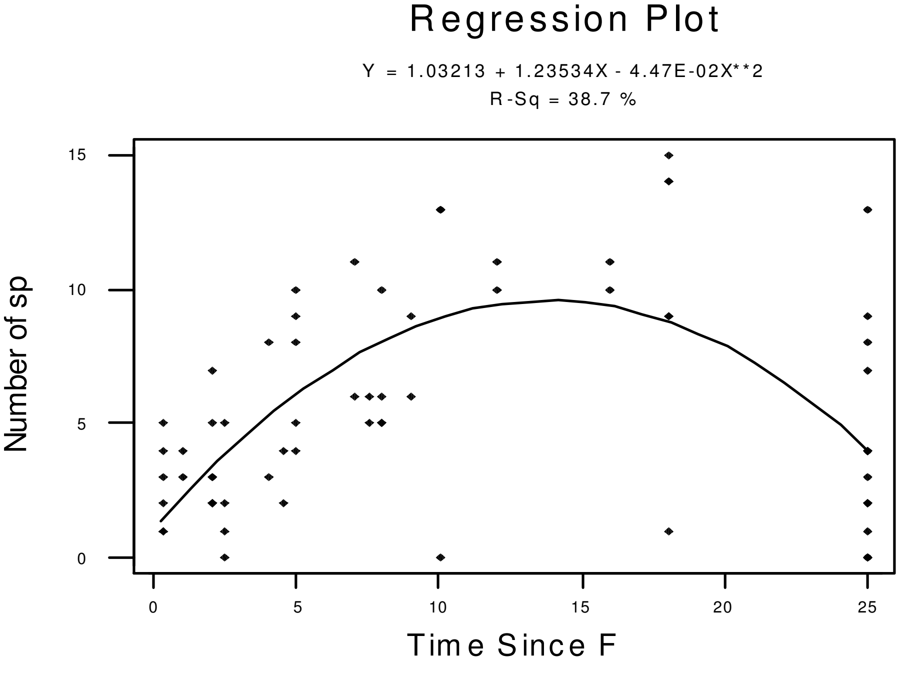

Fig. 4. Regression plot for lichen diversity in Area 1 excluding unburnt plots.

Neither of these graphs gives a truly accurate representation of the changes in diversity following burning. Fig. 4 shows increasing lichen diversity with time but that increases in diversity slow. It does not however give any indication that declines in diversity will be seen. Fig. 5 on the other hand includes information from older unburnt sites and clearly indicates that increases in diversity will be followed by declines after roughly ten years since burning. Again however this plot is probably not entirely accurate compressing changes in diversity into too short a time, failing to take into account the range of ages of unburnt stands and most importantly failing to reflect the true age of unburnt stands. Regression analysis was, as a matter of interest, also carried out on the data as a whole and the results can be seen in Appendix 7 (p. 92).

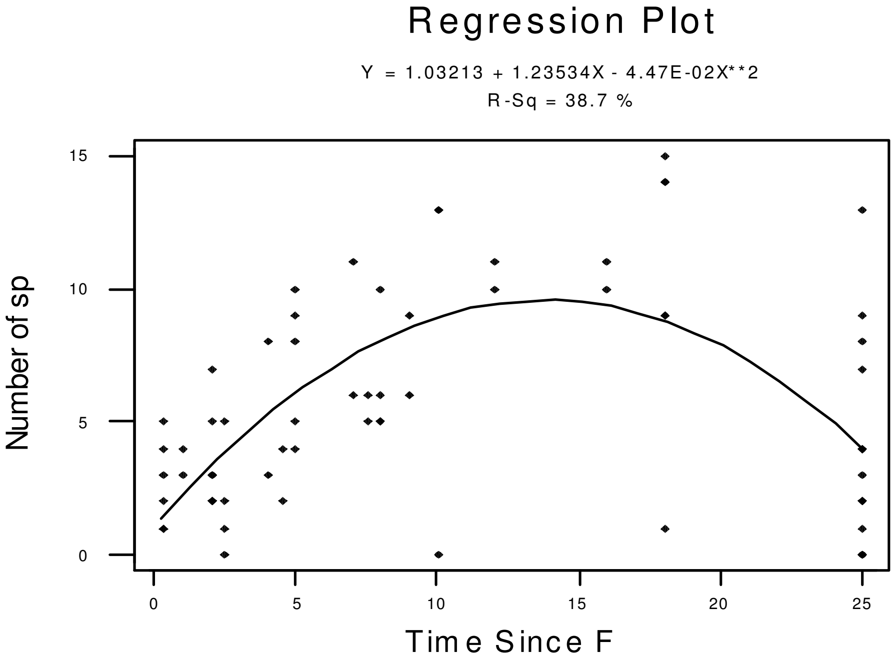

Fig. 5. Regression plot for lichen diversity in Area 1 giving unburnt plots an arbitrary value of 25.

iii. Changes in species composition

In the hypotheses it was postulated that changes would not just occur in lichen diversity but also that there would be significant changes in species composition creating a high β diversity. The following graph (Fig. 6) does not show all species present but gives an indication of trends by plotting the changing abundance of some key species. A comparison between the numbers of corticolous, terricolous and saxicolous species can be seen in Appendix 8 (p. 93).

The first graph while only showing four species illustrates the increasing importance of corticolous species in comparison to two relatively common terricolous species as stand age increases. Figure 7 in Appendix 8 shows the general trends in the diversity of terricolous, corticolous and saxicolous species. These graphs were prepared with data from areas one and two as area one was particularly poor in corticolous species.

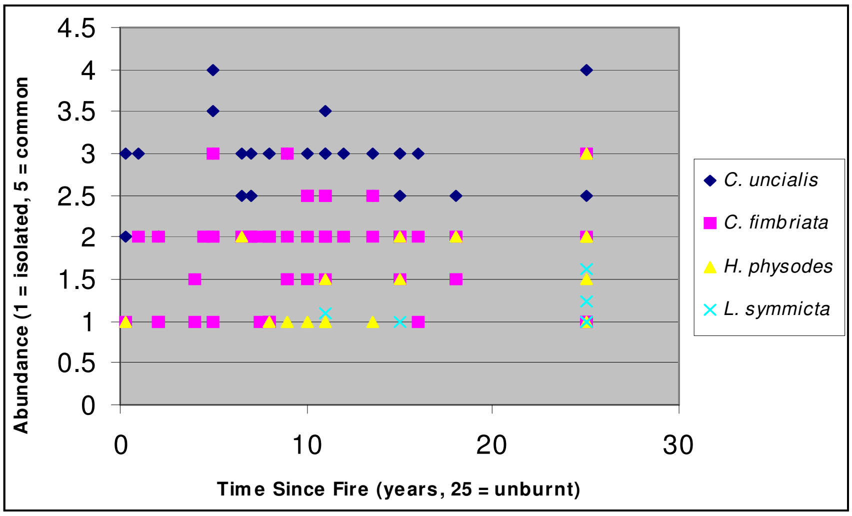

Fig. 6. Changing abundance of four lichen species.

C. uncialis and *C. fimbriata* = terricolous, *H. physodes* and *L. symmicta* = corticolous.

5.3 The Influence of Covariants on Lichen Diversity

i. Covariants related to changes in diversity.

Having examined the changing diversity of lichen species with regards to time since burning it is now necessary to examine the influence of covariants to determine if any factors other than the age of the stand influence lichen diversity. In order to do this a number of graphs were prepared plotting lichen diversity against time with environmental factors included as covariants. For most the results are ambiguous and the graphs can be seen in Appendix 9 (p. 94). The graphs showing the relationship of soil moisture and stage when burnt are of some interest however and can be seen below in Figures 7 and 8.

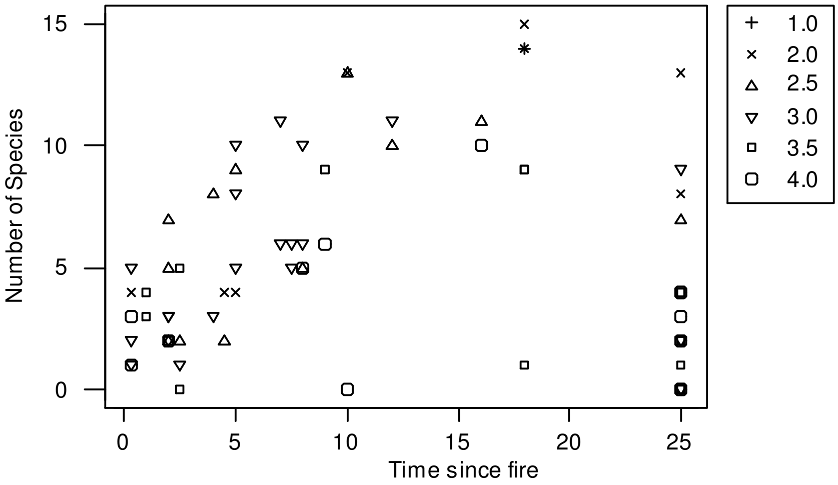

Fig. 7. Change in lichen diversity following burning related to soil moisture.

While neither graph shows anything particularly spectacular, it would seem from comparing Fig. 7 with the regression plots that areas with particularly high soil moisture are associated with lower than average lichen diversity. It is interesting to note that if one refers to the data on the differing environmental conditions between Areas 1 and 2 that area two is associated in general with drier soils and higher diversity, further suggesting a link between the two. Figure 8 which equates changing diversity with the stage at which the vegetation was burnt seems to suggest the possibility that lower diversity is found in stands that have been burnt later.

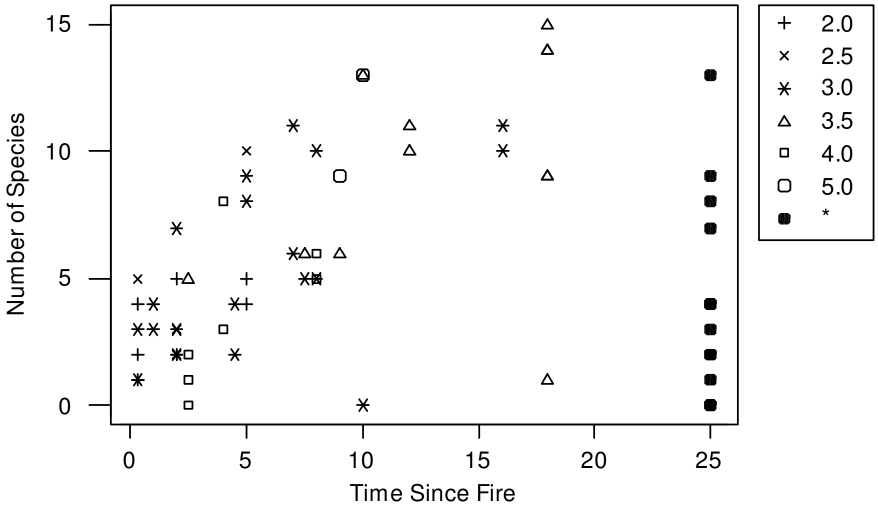

Fig. 8. Changes in Lichen diversity following burning related to stage when vegetation was burnt.

ii. Stepwise Regression Analysis

In order to further investigate the effects of covariants Stepwise Regression analyses were run in Minitab both for Area 1 and 2. No result was however obtainable for Area 2 due to insufficient data. Regressions were run including unburnt stands with an arbitrary age of 25 and excluding them. There was no difference between regressions including and excluding unburnt stands. Full results for the regression analyses can be seen in Appendix 5 (p. 88). The following were used as predictors: Quadrat number, aspect, altitude, slope, soil moisture, time since fire, fire intensity, Calluna stage when burnt and current *Calluna* stage.

For Area 1 the final equation including all significant predictors was as follows:

$$\text{No. Species} = 7.980 + (0.456 \times \text{age}) - (2.34 \times \text{moisture}) - (0.055 \times \text{quadrat no.}) + (1.14 \times \text{stage when burnt})$$

T-Values for the significant predictors were:

- Time since burning: 6.37
- Soil moisture: -4.13
- Quadrat number: -2.90
- Stage when burnt: 2.01

Quadrat number was included in the regression in order to investigate any potential bias in the investigation possibly due to increasing numbers of species identified through the investigation as the authors identification skills improved. In actual fact this is not the case as quadrat number is negatively correlated with species diversity. In order to remove the influence of quadrat number a second stepwise regression was run on the data from Area 1 using the same predictors but this time forcing time since burning and time since burning^2. Analyses were again carried out both including and excluding unburnt sites, again both sets of results were identical. A full set of results can be seen in Appendix 5. The final equation was as follows:

$$\text{No. Species} = 7.897 + (0.84 \times \text{time since fire}) - (0.022 \times \text{time since fire}^2) - (2.01 \times \text{moisture})$$

T-Values for these predictors were as follows:

- Time since fire: 3.49
- Time since fire^2: -1.69
- Soil moisture: -2.01

Both analyses, forced and unforced, were also carried out for the data as a whole and can be seen in Appendix 7 (p. 92). These again show the importance of the differences between Areas 1 and 2.

5.4 Detrended Correspondence Analysis (DCA)

DCA is an eigenanlysis method of indirect ordination based upon reciprocal averaging (Hill & Gauch 1980). It carries out ordination both of quadrats and species producing an ordination diagram which basically plots quadrats or species according to the similarity of their composition or occurrence. Analysis is carried out on the basis of the abundance of all species in the quadrats. This allows an interpretation of the underlying environmental conditions governing the distribution of quadrats/species in the ordination diagram (Kent

& Coker 1992). DCA analysis was carried out on the data as a whole, on Areas 1 and 2 separately and just for the lichen species. The species ordination plots can be seen in Appendix 10 (p. 95). The quadrat orientations are presented below.

In order to aid with the interpretation of these diagrams it was possible to subjectively delimit several groups which are included on the diagrams. Allowing comparisons between closely grouped plots as well as between those at opposite ends. Furthermore it was possible to overlay covariants onto these plots to aid with this interpretation.

In Figures 9 and 10, which show data from both areas there is a clear relationship between quadrat position in relation to Axis 2 and those covariants which are age determined. This suggests that position on Axis 2 is largely determined by the time when the quadrat was burnt. There is therefore a clear distinction between quadrats depending on the time when they were burnt.

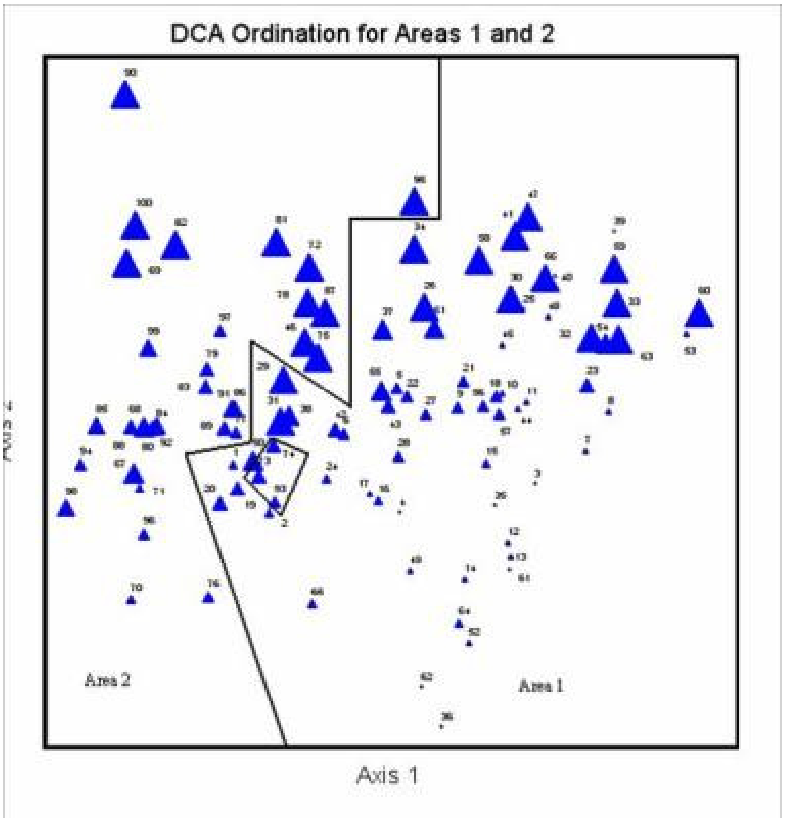

Fig. 9. Quadrat ordination for Areas 1 and 2 using time since burning as a covariant. Larger triangles relate to older plots. Areas 1 and 2 can be clearly separated.

Comparison with the raw data in Appendix 3. shows that there is also a clear general correlation between those plots which are older and lower lichen diversity. Location in relation to Axis 1 appears to be linked to soil moisture with those quadrats with higher soil moisture located towards the right and drier areas towards the left. It is interesting to note however that damper quadrats are located higher on Axis 2 suggesting that higher soil moisture is linked to older stands.

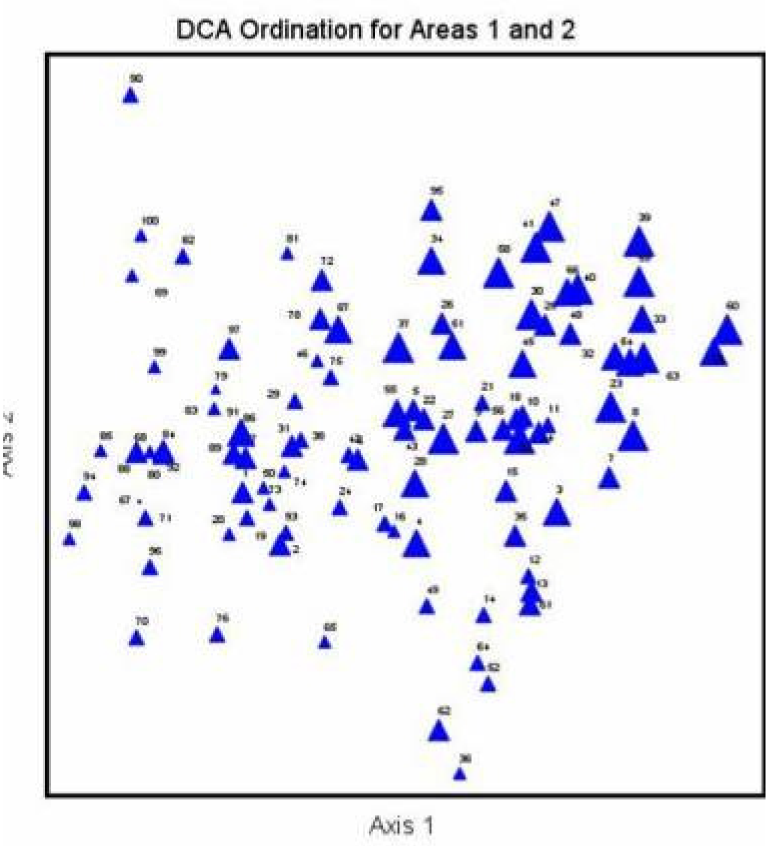

Fig. 10. Quadrat ordination for Areas 1and 2 using soil moisture as a covariant. Larger triangles correspond to higher soil moisture.

There is also a clear distinction between Areas 1 and 2 with each forming a distinct area in the diagram. Area 1 located to the right and Area 2 to the left. In figure 10. which includes data from both Areas there is also a clear distinction between those quadrats from Area 1 and those form Area 2 and the plot can effectively be divided in half with those plots from Area 2 on the left and those from Area 1 on the right. This axis is therefore also related to the differing composition of plants between the two NVC's which may therefore be a result of soil moisture. If each area is looked at separately lichen diversity can be seen to increase from right to left.

Higher soil moisture is found in Area 1. Quadrats closer to Area 2 plots show lower soil moisture, those plots in Area 2 with the highest soil moisture are in general located furthest to the right

Grouping and location on either axis is not strictly governed by time since burning or soil moisture however, but rather linked to changing species composition and abundance which is in turn largely a result of these two variables.

The plots for Area 1 (Figures 11 and 12) again show the importance of time since fire and soil moisture in defining species composition and abundance. Figure 12 shows that position in relation to axis one is strongly linked to soil moisture while Figure 11 shows position on axis two is defined by stand age. Again there is a link between older stands and higher soil moisture with damper stands located higher up Axis 2.

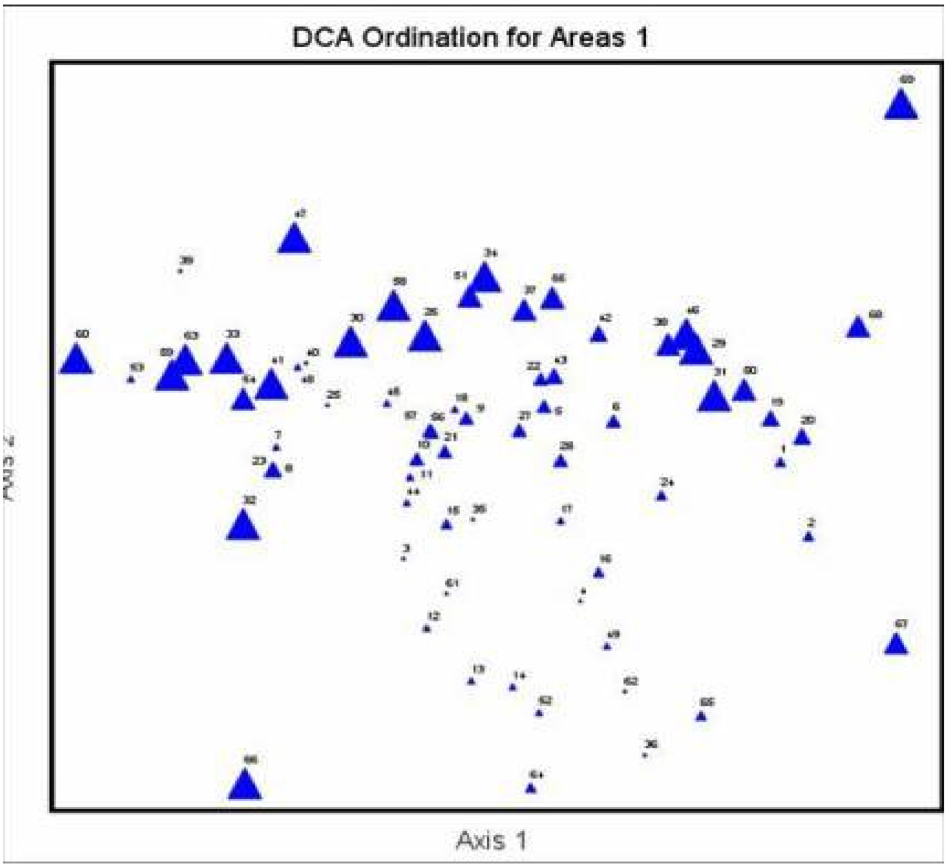

Fig. 11. Quadrat ordination for Area 1 using time since fire as a covariant. Larger triangles correspond to older stands.

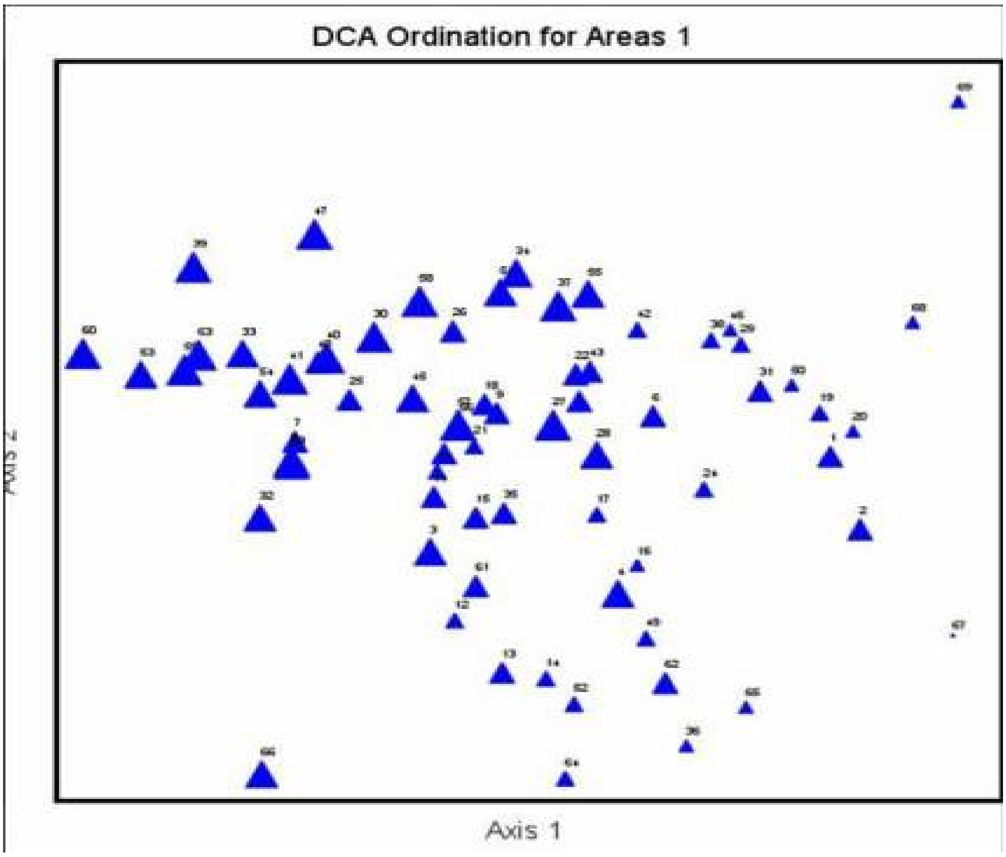

Fig. 12. Quadrat ordination for Area 1 using soil moisture as a covariant. Larger triangles correspond to higher soil moisture

The plots for Area 2 are unfortunately not so clear. Figure 13 below shows that there is a clear distinction between burnt and unburnt plots with the latter located towards the left of the plot. In burnt plots quadrats of different ages appear to be fairly well mixed together though clearly separate from those unburnt plots. This suggests that lichen diversity is maintained longer in Area 2 than in Area 1.

The plot for lichen species only gives a very clear grouping in the centre dominated by those quadrats which are dominated by a variety of terricolous lichens. Those plots to the extreme right are closely associated with quadrats of mainly terricolous species of low diversity and abundance and frequently with quadrats from recently burnt plots. Those to the extreme left however are quadrats with a high diversity and abundance of corticolous species with few terricolous species. Axis 1 can therefore again be linked to the time since burning and this is confirmed by Figure 14. Therefore in general recently burnt plots are located on the right and older plots on the left. Axis 2 is more difficult to define but is probably related to the diversity/abundance in each plot as opposed to the species composition. Axis 1 therefore defines composition, Axis 2 diversity/abundance within species groups.

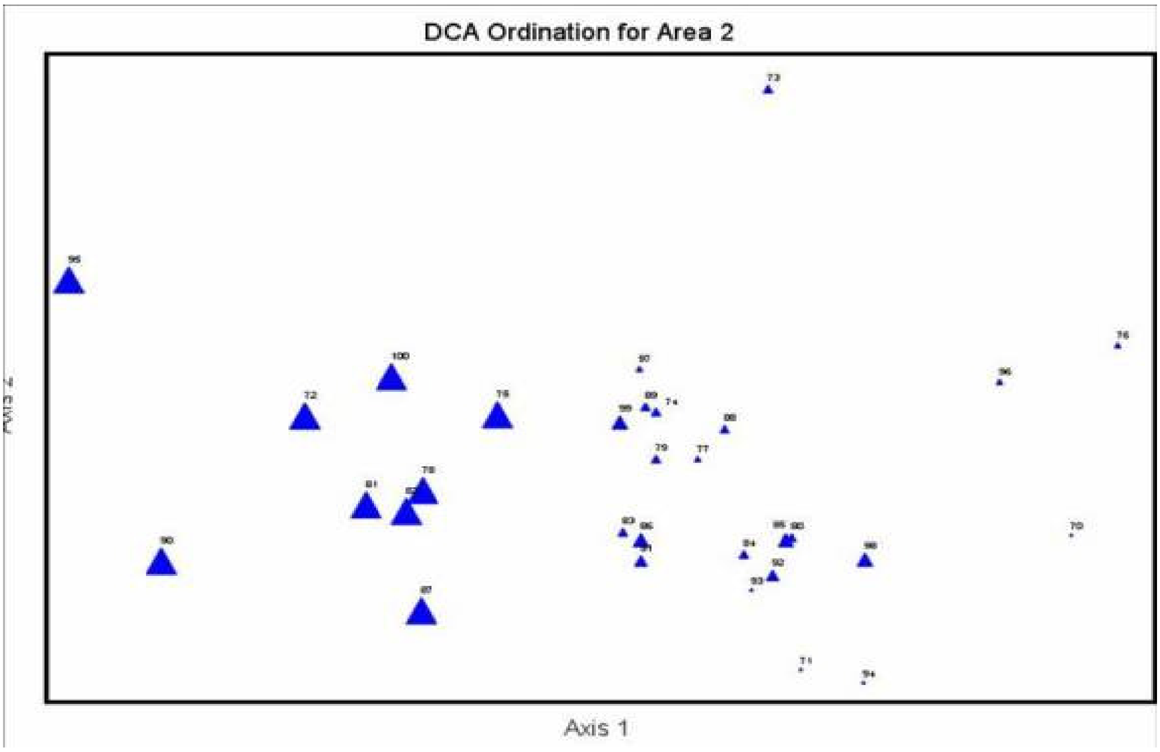

Fig. 13. Quadrat ordination for Area 2 using time since fire as a covariant. Larger triangles correspond to older stands.

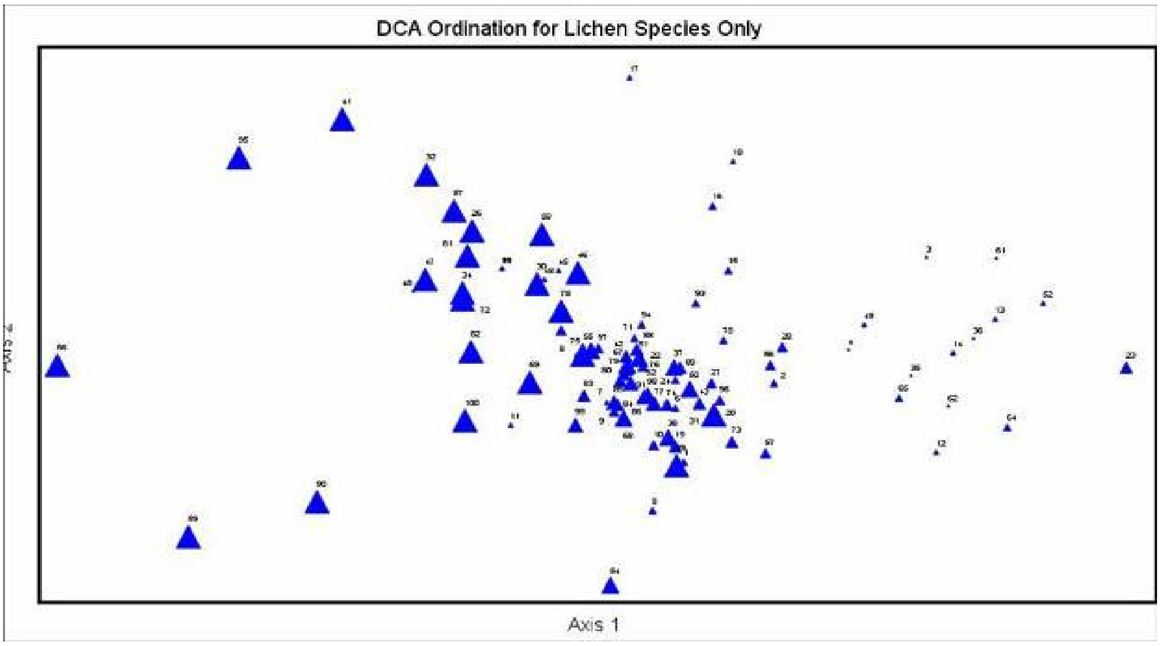

Fig. 14. Quadrat ordination for Areas 1 and 2 using only lichen species and time since fire as a covariant. Larger triangles correspond to older stands.

The plots for species relate different species in accordance to the frequency of their associations. Their position in the plot relates therefore largely to environmental parameters favoured by that species. These diagrams can be seen in Appendix 10 (p. 95). Interestingly for the information for the data for the plots for Areas 1 and 2 *Calluna* is located at the centre of the plot. Not only does this highlight its central position in these communities but it also allows the potential to relate location in the plot according to the conditions favoured by each species in relation to *Calluna* which may indicate the likely stage in which individual species will be found. Those species found closest to *Calluna* will possibly be those most commonly associated with periods of *Calluna* dominance. Unfortunately there is insufficient time to study this in any detail and it is possibly a topic for future study.

5.5 Ellenberg Numbers

In Section 2 of this paper it was stated than an objective would be to produce as series of Ellenberg numbers for lichens. These numbers are subjective and define a plants environmental preferences in terms of demand for light, temperature, moisture, continentality, nitrogen and pH. Numbers do not currently exist for lichens. A set was however created by Dr. C. Legg by taking the NVC's in which each species was recorded to occur (this also is by no means complete for lichens) and averaging out the Ellenberg numbers for the species that were located in those NVC's. Ellenberg numbers were also created for each of the quadrats using the numbers already available and those generated for lichen species by the method described above. Averages were taken from the values for all species in the quadrat for each of the variables. The values were weighted according to dominance in the NVC and according to dominance in the quadrat. It is recognised that by using averages for all species values for light and temperature will be largely useless as they include entirely different groups of species including canopy forming species such as *Calluna* and those located at the ground layer beneath a fully grown canopy, for example pleurocarpous mosses. The latter favour the damper darker conditions created by *Calluna* microclimate. The values for Nitrogen (N) and Reaction (R)[*] should however still be useful. The quadrat scores for N and R were therefore plotted against time since burning. Areas 1 and 2 were plotted separately. As can be seen from Figures 15 and 16 there is a clear association between groups of species preferring more N rich conditions and newly

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[*] Related to pH: higher R corresponds to higher pH

burnt stands. The N demand of communities declines with time from burning. It also seems, rather oddly, that earlier communities prefer more alkaline conditions.

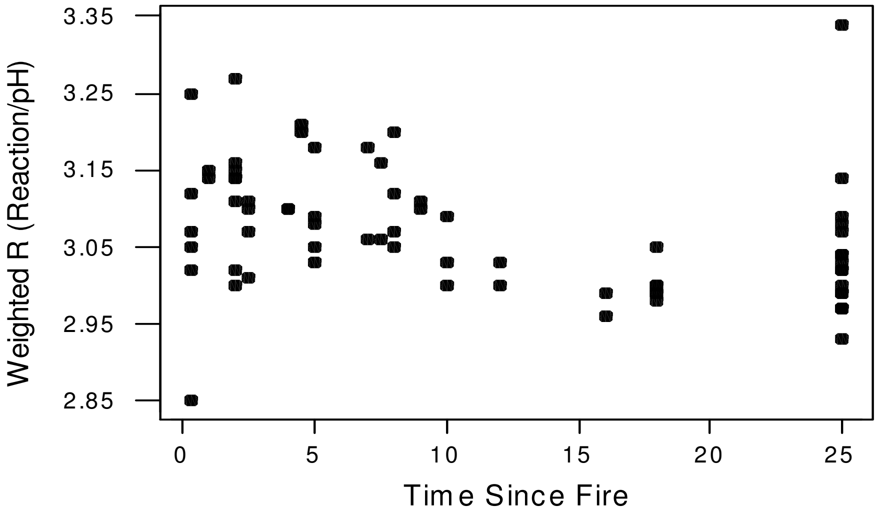

Fig. 15. Ellenberg R of quadrat communities related to time since burning

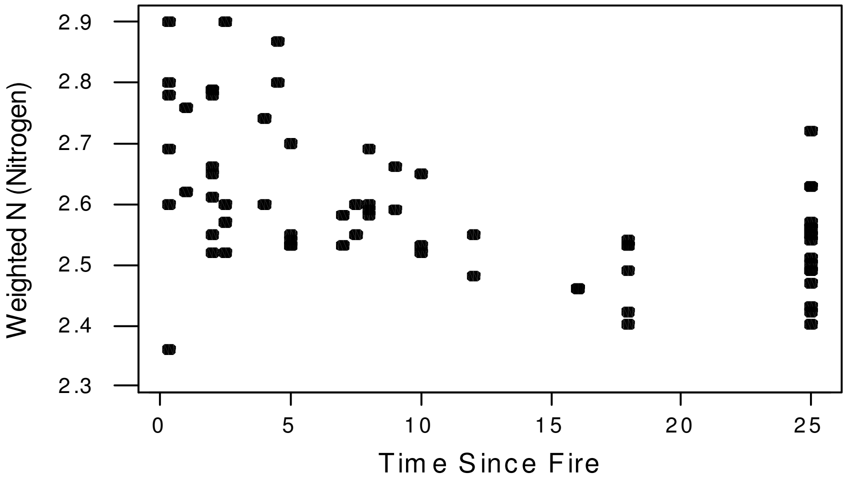

Fig. 16. Ellenberg N of quadrat communities related to time since burning

6. DISCUSSION

Having examined and analysed all the results and statistical information it is now possible to examine a number of points that they raise.

The first clear observation it was possible to make was that there was a significant difference between Areas 1 and 2. It was obvious even during the fieldwork stage that there was a greater diversity of lichen species in Area 2 than in Area 1 and that diversity was maintained for longer, even into the late building phase. The two areas are of course different NVC's, nevertheless the great differences between the two regarding their lichen diversity came as something of a surprise. The differences between the two areas in terms of lichen species richness can largely be seen to be a result of their differing environmental conditions. Area 2 has been shown to be much drier with thinner more stony soils. This has allowed the development of *E. cineraea* as a co-dominant species but also has created conditions less suitable for the growth of mosses, in particular those pleurocarpous mosses which thrive beneath the *Calluna* canopy. The microclimate exerted by the *Calluna* is also not so strong in Area 2 with the drier conditions leading to less luxuriant growth and a more patchy, open canopy. *Calluna* bushes are also in general smaller in Area 2 than those of the same stage in Area 1. The differences in these conditions has effectively allowed lichens to maintain their dominance over much of the area effectively filling the niche occupied by pleurocarpous mosses in Area 1 and forming dense mats dominated by *C. portentosa* and *C. arbuscula* beneath the *Calluna* canopy. The GLM demonstrated the significance of the differences between the two areas showing that this was the most important factor controlling lichen diversity.

It is also interesting to note that there were a large number of lichen rich patches (see Figure 17 below) devoid of any other vegetation in Area 2. In a number of quadrats this contributed to a significantly higher diversity of lichens than would have been found under a complete canopy. This was most common in Area 2 where these patches, possibly caused by the inhibition of germination described by Lawrey (1977) and Hobbs (1985), occurred relatively frequently even amongst building and mature *Calluna*.

Fig. 17. A Lichen rich patch in Area 2, in an otherwise closed *Calluna* and *Erica* canopy

In Area 1 areas of higher lichen diversity were found in building and mature quadrats that were crossed by deer tracks. The trampling effect opening up gaps in the *Calluna* canopy, breaking up moss mats and allowing lichen species to colonise the track edges.

The second observation that can be made is that there is a clear trend of increasing lichen diversity following burning. The difference between Areas 1 and 2 meant that analysis largely had to be carried out on each area separately. This unfortunately meant that there was little information for middle-aged stands in Area 1 and no information for stands younger than 6 years in Area 2. For Area 1 however it is clear from the regression analysis that lichen diversity increases following burning reaching a maximum after 15 years or so. Neither of the fitted line plots represent the true changes following burning with Figure 4 failing to take into account declines in older stands and Figure 5 compressing the time period over which these changes occur. Although such regressions were not possible for Area 2 it appears from Figure 3 that there may be a similar trend in Area 2 albeit to a lesser extent and possibly over a greater time period. The decline in diversity is largely caused by the changing conditions at ground level. Mallik (1986) has described the changing conditions below the *Calluna* canopy following burning. Below a building phase canopy light is reduced, and a more humid atmosphere is created with less water loss by evaporation from the soil. This favours the growth of mosses which eventually largely replace lichens at the ground layer. Some bryophilous species such as *C. portentosa*, *C. crispata* and *C. squamosa* may remain but most species will be replaced. The notable exceptions to these declines are the corticolous species which are able to colonise the older woodier branches of building-mature *Calluna*. There again appears to be a difference between Areas 1 and 2 with *P. physodes* the only common corticolous species in Area 1 as opposed to the greater diversity in Area 2. Again this difference may be related to the differing environmental conditions between the two sites. These observations go against the traditional wisdom from papers such as Barclay-Estrup and Gimingham (1969) and Coppins and Coppins (2001) which state that highest lichen diversity is found in degenerate and mixed-age *Calluna*. This investigation agrees therefore with Sanderson (1996), Hobbs and Gimingham (1984) and Ward (1970) and shows that burning does not necessarily negatively affect lichen diversity and may even allow for higher lichen diversity than would be found in unburnt heathland.

Time since burning is not however the only control on lichen diversity. The analysis shows that soil moisture is significant in Area 1 while the stepwise regression also found that stage when burnt was significant. The influence of soil moisture is however not as simple as it may seem as it may in fact be related to the age of the stand. The DCA analysis showed that there is indeed an apparent link between stand age and soil moisture. It has already been stated that a dark, damp microclimate is created beneath the building-mature *Calluna* canopy. However higher soil moisture encourages the growth of bryophytes and where mats of pleurocarpous mosses survived following burning lichen colonisation was notably reduced making it surprising that fire intensity was not significant. This however was only the case in a limited number of cases and sites with surviving moss mats generally also had damper soils meaning these quadrats may also be included in the overall significance of soil moisture as a covariant. The significance of soil moisture may therefore be masking the importance of other variables. In the first stepwise regression, stage when burnt was also significant. This brings the idea of initial floristic composition into the equation. Stands which are older when burnt appear to have a significantly higher number of species than those burnt when younger. It may be that older stands may have a higher number of species before burning and as is pointed out on the USDA website *Cladonia* species may survive burning in sheltered places or where they are protected by moss mats. Thus there may be more species present to survive burning or bryophilous species under older *Calluna* may be protected by damp moss mats and litter, which will also be more common. This may allow these species to survive burning and be found in areas in which one would not expect them.

The significance of quadrat number was investigated for reasons that have already been explained. It was not however expected that it would be significant in defining diversity and certainly not expected that higher quadrat numbers would be associated with <u>lower</u> diversity. In retrospect this can probably be explained by the fact that many of the later quadrats investigated in Area 1 were unburnt and therefore of lower diversity. For this reason it was sensible to remove this influence by forcing time since burning and time^2 to produce a workable predictive equation with time since burning and soil moisture as the significant predictors.

The Detrended Correspondence Analysis produced an interesting set of results, once again highlighting the importance of time since burning as the key controlling factor in lichen diversity. All the DCA's showed that significant difference exists between burnt and unburnt stands with the latter located in clearly demarkable groups. Figure 9 reinforces the view that Areas 1 and 2 are significantly different. The significance of soil moisture is also confirmed by the DCA analysis which showed a clear demarcation of quadrats according to soil moisture levels. The DCA highlights the fact that quadrats in old mature-degenerate stands and in those that have been recently burnt have significantly lower diversity than those in stands aged 12-20 years old do. In the DCA for lichen species only the large grouping of quadrats in the centre are those of intermediate age and highest lichen diversity. Those at the extremes of the diagram are those quadrats which are either unburnt of very recently burnt with low diversities of mainly terricolous and corticolous species respectively.

These results confirm what was hinted at by Sanderson (1996) and questions the current wisdom on the role of lichen species in *Calluna* heathland ecology. Previous papers, such as Barclay-Estrup and Gimingham (1969), which have dealt with the ecology of lichen species albeit in passing frequently state that highest lichen diversity will be found in the degenerate phase as the *Calluna* canopy opens up. The results from Area 1 show that on the whole this is simply not the case. While some unburnt stands do exhibit high diversity the highest is found in stands 12-20 years old with lichen diversity increasing fairly rapidly following burning. Closure of the *Calluna* canopy leads to changing microenvironmental conditions and the dominance of pleurocarpous mosses which form large all-covering mats. This limits lichen species to a few bryophilous species. The species ordination plot for Area 1 (see Appendix 10) shows that the pleurocarpous mosses and the majority of lichen species are grouped separately indicating the differing conditions favoured by each group. The fact that the canopy opens up in the degenerate phase does not allow for the re-establishment of terricolous species to any great extent. What does happen however is that the thick woody stems and opening canopy allows for colonisation by corticolous species, in particular *P. physodes*. In Area 1 however this does not happen to the same extent as in Area 2.

Area 2 has been shown to be significantly different form Area 1 and this shows that possibly the most important factor in determining diversity are the underlying environmental conditions. While data is lacking for sites younger than 6 years it appears that Area 2 follows the same general trend although lichen diversity is consistently higher than in Area 1. Mosses especially pleurocarpous species are conspicuous through their absence and it appears that the drier conditions have allowed lichens to fill this niche. Corticolous species in particular are much more common than in Area 1. Lichen rich patches where the regeneration of *Calluna* has been prevented are also significant.

The information provided by the “Ellenberg” data should not be regarded as particularly reliable especially as the weighted numbers used to compile Figures 15 and 16 were is some cases only based on the value for a single species while for other quadrats data was available for all species. It does however show that communities found after burning seem to be those which respond favourably to higher N availability which would be present following burning due to the deposition of nutrients previously locked up in biomass. The information on R certainly does not seem to agree with previous data for post fire conditions by authors such as Southorn (1977) who state that pH is significantly lower following burning. This area clearly requires further research but suggests that burning communities following burning may not just be responding to the destruction of the *Calluna* canopy and the opportunities this presents but to a wider range of changes and that the pathways of regeneration may also be responding to changes in these conditions.

6.1 Implications for Management

These results reveal that areas of the estate are relatively species rich in lichens. The fact that 22 species of *Cladonia* were found in one two-week survey suggests that the estate may possibly rival the famously rich Muir of Dinnet NNR. The results also suggest that muirburning is instrumental in maintaining high lichen diversity. This is not to suggest however that all areas should be burnt in order to raise lichen diversity even if this was the primary aim for future management. β diversity across both areas is significantly higher than α diversity meaning that in order to maintain the highest possible diversity throughout the estate it is necessary to maintain a range of sites of different ages. Burning allows the formation of areas of young vegetation with high lichen diversity. Burning is probably required more regularly in Area 1 since in Area 2 high diversity is maintained longer and continues even into the building and mature phase heather under a largely closed canopy albeit one thinner than found in Area 1. There are a number of points which this investigation has unfortunately failed to show and one of the most important is these is the diversity of saxicolous species found on the scree and rocky outcrops scattered throughout both areas (see Figures 18 and 19 below). The nature of the sampling strategy and probably the location of burns by gamekeepers means that areas such as these were not included in the areas being sampled. The presence of these species means that lichen diversity in both Areas 1 and 2 is likely to be much higher than suggested in this study.

Fig. 18. (left) shows lichen covered scree in Area1. Fig. 19. (right) shows a rocky outcrop in Area 2.

The lichens found in these areas are likely to be slow growing species which would be greatly damaged and probably killed were fire to pass through their area. The length of time it would take for these species to recover and reach their former diversity and abundance is likely to be in the hundreds of years. It is essential that such areas are therefore avoided.

Greatest lichen diversity is found in Area 2 which is important as this is an areas of the estate where both muirburning and grazing has been stopped with the aim of allowing woodland regeneration. Not only does this not bode well for lichen diversity in the area but it would seem in fact that, as far as lichen species are concerned, this area would ideally be the one in which muirburning continued. It is interesting to note that during the course of the study no woodland regeneration was observed in Area 2 even at the margins of remnant scrub and forest areas. It is possible that the high cover of lichens in these areas is preventing the establishment of seedlings. Unburnt heather in this area is likely to maintain carpets of lichens beneath its canopy possibly giving way to mosses later on. These conditions together with absence of grazing by any large animals means that there is very little disturbance that might allow the establishment of woodland or scrub species. This theory is confirmed by the authors observations in the field. While there was no obvious regeneration in Area 2, in Area 1 however seedlings of *Sorbus aucuparia* were frequently observed and one was even recorded in a quadrat. It should be kept in mind that this is the area in which both burning and grazing continues. All of this points to a need for further investigation of the status of the estates moorlands and a possible reappraisal of current management practice.

7. SUMMARY

This paper has examined the impact of muirburning on lichen diversity. It is possible to conclude that this study has shown that far from the destructive management tool it is frequently viewed as muirburning in fact is an essential part in maintaining high lichen diversity. There are however significant differences in the diversity of different areas depending largely on the underlying environmental conditions. There are currently very few other papers examining the ecology of lichens on moorland and the effect of burning on their diversity. Hopefully this paper has served to draw attention to an area which requires further investigation. There is clearly a need to collate far more data than was possible in the scope of this study. Even here it has not been possible to examine all the areas possible and there is substantial scope for investigations into individual ecology of lichen species and their associations. Further, more detailed investigations of the environmental conditions underlying different habitats and the resulting differences in diversity, regeneration pathways and speed and the maintenance of lichen diversity would also be of benefit. Indeed a study similar to this one but on a greater scale which could possible iron out the various biases in sampling strategy, identification and other problems that exist with the data used here would also be of benefit.

GENERAL DISCUSSION

Having completed both papers in is now possible to make a number of general conclusions. It has been demonstrated that the controlling factor in the ecology of heathlands is the life cycle of *Calluna* from small pioneer plants through the closed canopy of the building phase to the increasingly open conditions of the mature and degenerate phase. The dominance of *Calluna* and the microclimate it creates beneath its canopy means that it has great impact on the diversity and abundance of sub-canopy shrubs and ground layer plants.

The process of muirburning curtails the natural progression of *Calluna* through this cycle and aims to maintain the pioneer and building phases to produce higher quality grazing for sheep, deer and grouse. Little literature is available that studies in detail the effects of these processes on lichen diversity. Burning normally destroys lichens and most management fires will normally be enough to kill off the vast majority of plants. Regeneration following burning is however rapid and even more so where individuals have survived fire possibly due to protection by litter, damp moss mats or due to their sheltered locations. In contrast to what some literature states the degenerate phase does not appear to be the period of highest lichen diversity. This seems occur some 15-20 years following burning when there has been a long enough time period for regeneration and for colonisation but the full effects of the *Calluna* canopy have not yet impacted on the ground layer flora. Normally this influence seems to favour the formation of mats of pleurocarpous mosses, largely at the expense of lichens.

Some authors have written of the importance of the nature of fire conditions and the importance of initial floristic composition in determining the pathways of vegetation development following burning. While “age when burnt” came out as a significant variable in one analysis further investigation is needed to determine the ways in which the age of stand affects the later diversity of lichens following burning. It is suggested here that a possible explanation may be the survival of individual protected from the fire by litter and moss mats. Information on fire intensity is not particularly reliable as this was judged on the basis of litter left-over following burning and obviously in older stands smaller pieces of litter will have rotted away introducing a serious bias into this variable. The practical paper has however confirmed the importance of the life-stage of *Calluna* in determining lichen diversity and it is possible to summarise changes in lichen diversity on burnt moorlands as follows:

- Low diversity/absence immediately following burning.
- Increasing diversity reaching a maximum 15-20 following burning.
- Decreasing diversity in the building phase onwards.
- Increasing abundance of corticolous species in the building-degenerate phases
- Decreasing abundance of terricolous species over the same period.

The practical study also showed the importance of underlying environmental conditions in determining lichen diversity and that there is great variation in diversity and regeneration pathways between communities. There is scope for much wider study including:

- Studies on a wider range of communities.
- Experimental burning to allow accurate observation of initial floristic composition and fire conditions.
- More detailed studies on changes in species composition comparing data with species tolerances (See Literature Review Appendix 2 p. 37).

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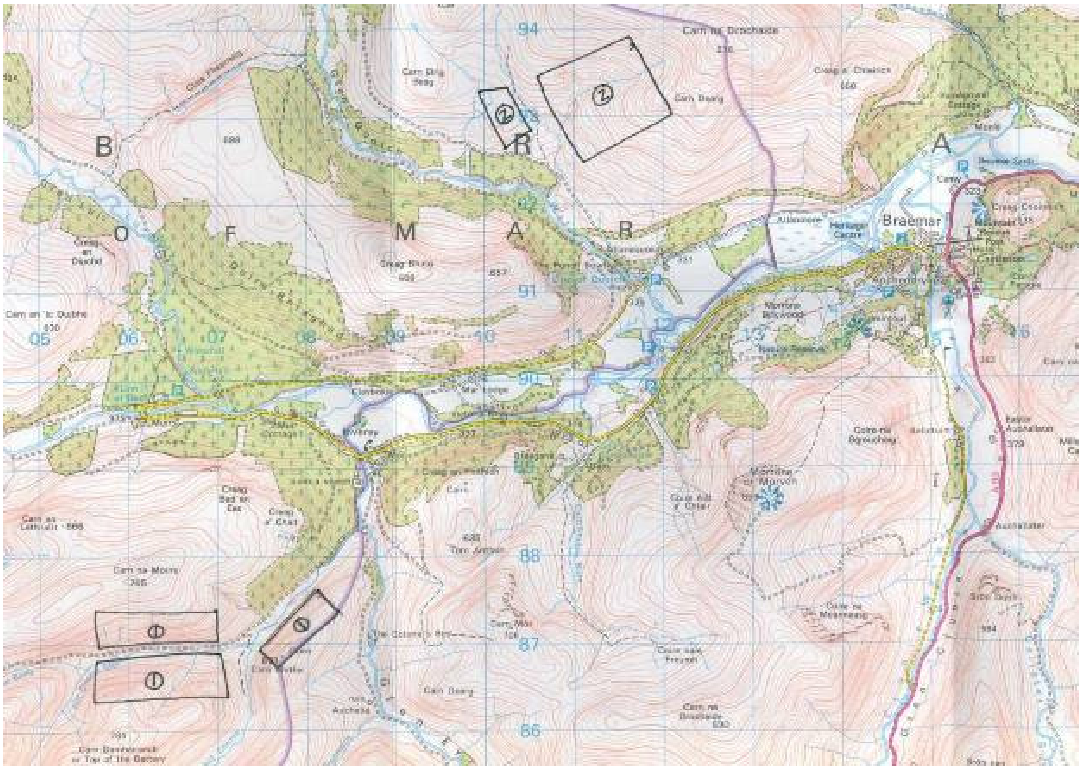
APPENDIX 1

Below are photographs of the burns studies in Areas 1 and 2 and a 1:50,000 map showing the location of the study areas in relation to Mar Lodge. Maps of the burns at 1:10,000 scale can be seen in the following pages.



O/S Map (originally 1:50,000) Showing the location of Mar Lodge and of Sampling Areas 1 and 2

Photograph of Sampling Area 1, looking towards Carn Bhithir.

The Eastern end of Carn Bhithir in Area 1.

Sampling Area 1, looking towards Carn na Moine.

Sampling Area 2, looking towards Carn na Criche.

APPENDIX 2

Arbitrary Scales Used to Define Covariants

- Slope
    1. Very Slight
    2. Slight
    3. Moderate
    4. Steep
    5. Very Steep
- Soil Moisture
    1. Very Dry
    2. Dry
    3. Damp
    4. Wet
    5. Very Wet
- Fire Intensity
    1. Very Low
    2. Low
    3. Medium
    4. High
    5. Very High
- Calluna Stage
    1. Pioneer
    2. Building
    3. Mature
    4. Degenerate
    5. Mixed Age Stand

APPENDIX 3

Raw Data

The following pages show spreadsheets containing raw data, including the environmental parameters and the abundance and diversity of vascular plants, bryophytes and lichens, from each quadrat. As well as the weighted “Ellenberg” numbers for each quadrat. The list below shows quadrats with significant features.

3: Crossed by deer track
7: Little regeneration of *Calluna*
10: *E. tetralix* patches, open patches with little regeneration
11: Moss mat burnt away
13: Rocky area, thinner soil
15: Small fire, rocky
16: Variation in temp over area
17: Quadrat at edge of burn
19: Near gryke and stony area
24: Stony, scree, patchy regeneration.
27: Small fire
33: Near gryke
35: Quadrat crossed by deer track
36: Rocky, thin soil
38: Large gap in *Calluna* canopy
42: Large rock partly in quadrat
44: Thin soil
45: Dry, thin soil, near plateau
50: Rocky outcrops
51: Rocky outcrops
52: Thin soil, stony
55: Rocky thinner soil
61: Top layer of soil scorched
62: Top layer of soil scorched
63: Valley bottom, pionner-degernerate *Calluna*
64: Mixed stages, quadrat in hollow
65: Stony ground

67: V. stony and dry

70: Thin stony soil

75: Pioneer-degenerate *Calluna*

76: V. grassy area

82: Building-degenerate *Calluna*

83: Edge of burn, lichen rich *Calluna* free patch

84: Lichen rich patch, crossed by deer track

85: Rocky outcrops

89: Patches of bare earth

90: Patchy canopy

91: Co-dominance of *V. vitis-idaea*

93: Co-dominance of *V. vitis-idaea*

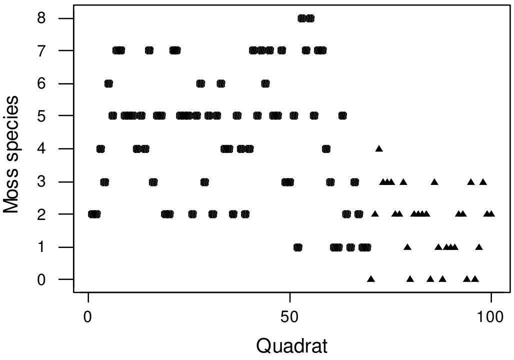
94: Lichen rich, shrub free patches

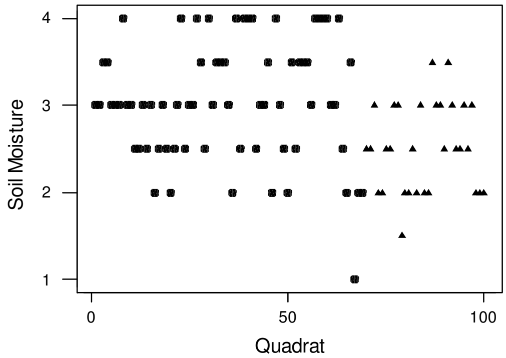
96: Lichen rich, shrub free patches

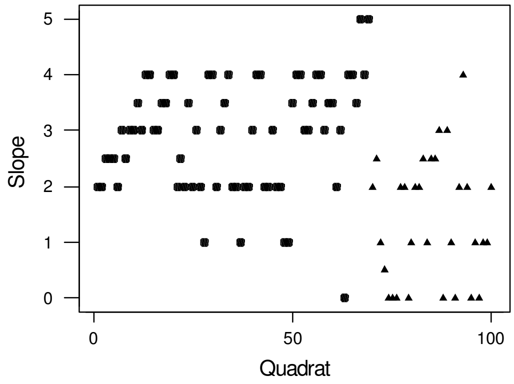
97: Bottom of gulley, thin open canopy

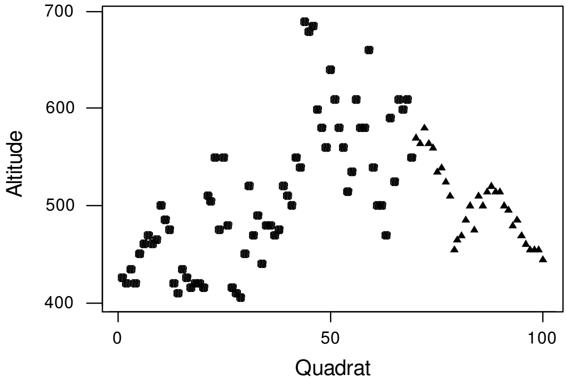
APPENDIX 4

The following graphs show the differing environmental conditions in Areas 1 and 2. Each graph plots a particular environmental parameter against quadrat number. Quadrats 1-69 = Area 1, Quadrats 70-100 = Area 2. • = Area 1, ▲ = Area 2.









APPENDIX 5

Below can be found the print outs from Minitab for the various regression analyses carried out. Results for the Stepwise Regression were the same whether unburnt data was included as aged 25 or excluded.

General Linear Model for Areas 1 and 2 Combined

Using unburnt = 25

```
Factor     Type Levels Values

Analysis of Variance for Number o, using Adjusted SS for Tests

Source     DF     Seq SS     Adj SS     Adj MS       F      P
Quadrat     1     509.60      39.40      39.40    5.66  0.020
Altitude    1      53.11       0.03       0.03    0.00  0.952
Slope       1       3.43       0.44       0.44    0.06  0.803
Soil Moi    1     172.77      54.11      54.11    7.77  0.007
Time Sin    1     359.77      97.57      97.57   14.01  0.000
Fire Int    1       5.50       3.50       3.50    0.50  0.481
Stage Wh    1      45.55      27.61      27.61    3.97  0.051
Current     1       2.48       2.05       2.05    0.29  0.589
Area        1     131.17     131.17     131.17   18.84  0.000
Error      64     445.61     445.61       6.96
Total      73    1728.99

Term           Coef     StDev        T      P
Constant     -1.320     4.570    -0.29  0.774
Quadrat    -0.05456   0.02294    -2.38  0.020
Altitude -0.000366  0.006003    -0.06  0.952
Slope        0.0807    0.3229     0.25  0.803
Soil Moi    -1.5591    0.5593    -2.79  0.007
Time Sin     0.4817    0.1287     3.74  0.000
Fire Int     0.4116    0.5801     0.71  0.481
Stage Wh     0.9952    0.4997     1.99  0.051
Current      -0.579     1.066    -0.54  0.589
Area          6.798     1.566     4.34  0.000

Unusual Observations for Number o

Obs  Number o       Fit   StDev Fit  Residual   St Resid
 23    0.0000    6.2385      1.0633   -6.2385     -2.58R
 54    1.0000    9.4821      0.9517   -8.4821     -3.45R

R denotes an observation with a large standardized residual.
```

Stepwise Regression for Area 1

Using unburnt =25

```
 F-to-Enter:       4.00    F-to-Remove:      4.00
```

```
 Response is Number o on  8 predictors, with N =   52
 N(cases with missing observations) =  17 N(all cases) =   69


    Step        1        2        3        4
Constant     2.737    8.783   10.317    7.980

Time Sin     0.483    0.452    0.506    0.456
T-Value       6.47     6.56     7.29     6.37

Soil Moi              -1.98    -2.12    -2.34
T-Value               -3.32    -3.71    -4.13

Quadrat                       -0.046   -0.055
T-Value                        -2.42    -2.90

Stage Wh                                 1.14
T-Value                                  2.01

S             3.03     2.76     2.64     2.56
R-Sq         45.56    55.56    60.39    63.51
```

Stepwise Regression for Area 1

Using unburnt = 25, forcing time since burning and time ^2

```
 F-to-Enter:      4.00    F-to-Remove:      4.00


 Response is Number o on  9 predictors, with N =   52
 N(cases with missing observations) =  17 N(all cases) =   69


    Step        1        2
Constant     1.824    7.897

Time Sin      0.86     0.84
T-Value       3.21     3.49

Time Sq     -0.021   -0.022
T-Value      -1.46    -1.69

Soil Moi              -2.01
T-Value               -3.42

S             3.00     2.71
R-Sq         47.82    58.06
```

Polynomial Regression for Area 1

Using unburnt = 25

```
Y = 1.03213 + 1.23534X - 4.47E-02X**2

R-Sq = 38.7 %


Analysis of Variance
```

```
SOURCE            DF         SS         MS         F         P
Regression         2     434.55    217.274   20.8465  9.61E-08
Error             66     687.89     10.423
Total             68    1122.43


SOURCE      DF    Seq SS         F         P
Linear       1    12.045  0.726787  0.396964
Quadratic    1   422.502   40.5374  2.13E-08
```

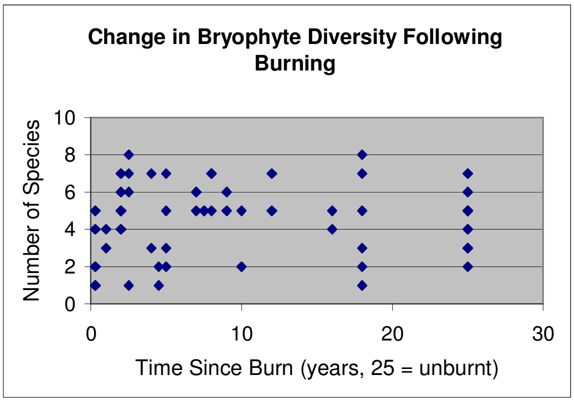
Polynomial Regression for Area 1

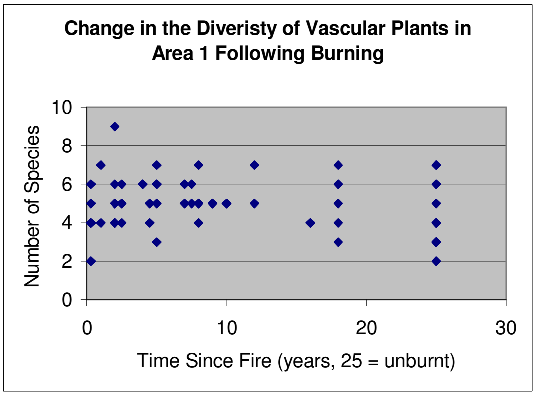
Using unburnt = *

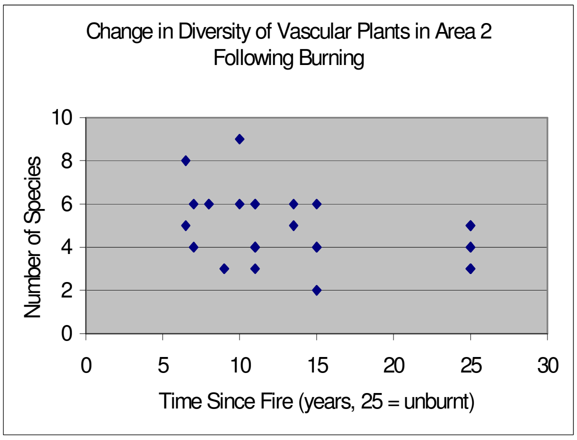
```
Y = 1.82351 + 0.856595X - 2.07E-02X**2

R-Sq = 47.8 %


Analysis of Variance


SOURCE            DF         SS         MS         F         P
Regression         2    403.074    201.537   22.4565  1.20E-07
Error             49    439.753      8.975
Total             51    842.827


SOURCE      DF    Seq SS         F         P
Linear       1   384.031   41.8520  4.06E-08
Quadratic    1    19.043   2.12184  0.151590
```

APPENDIX 6

The graphs below plot the diversity of mosses and vascular plants against time since burning. The graph for bryophytes only shows data from Area 1, the scarcity of mosses meant that the graph for bryophyte diversity in Area 2 was of little interest. Separate graphs for vascular diversity exist for Areas 1 and 2.

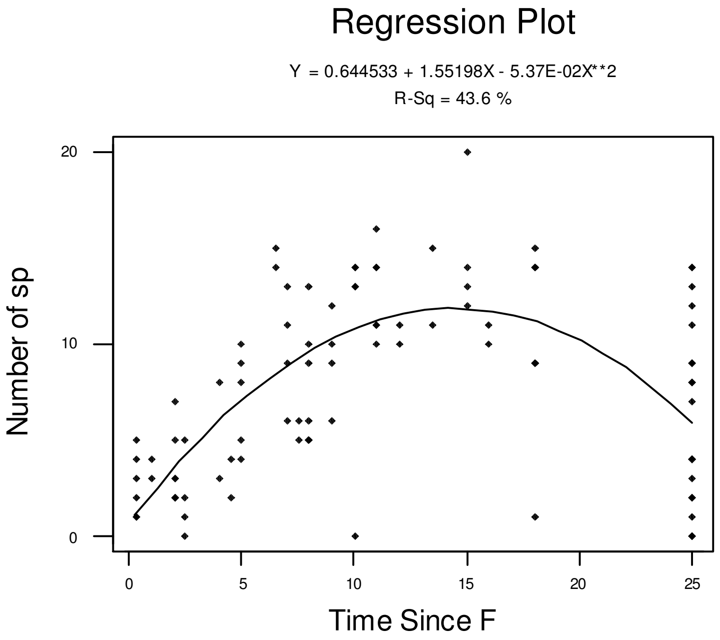






APPENDIX 7

Below are the fitted line plots for the data as a whole. Although fairly similar to those for Area individually they were not analysed in the text due to the significance of the differences between Areas 1 and 2. They are included here simply for reference.

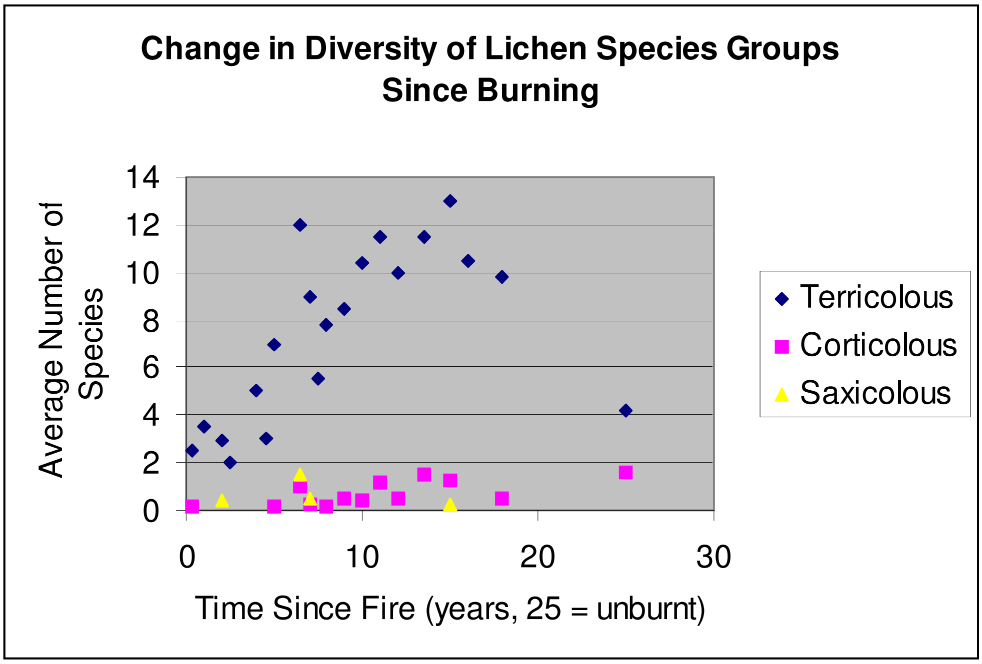


Fitted line plot for all data including unburnt stands have been given an arbitrary age of 25.

Fitted line plot for all data excluding unburnt stands.

APPENDIX 8

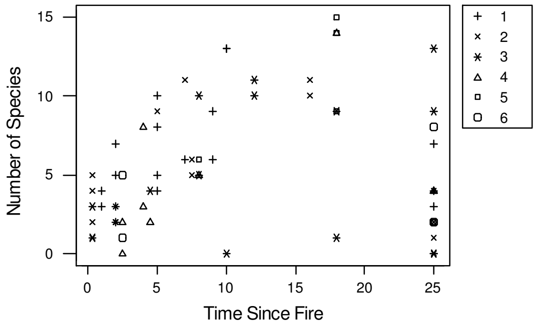
The graph below plots average diversity of terricolous, corticolous, and saxicolous species in quadrats of the same age against time since fire. The graph uses data from both Areas 1 and 2.



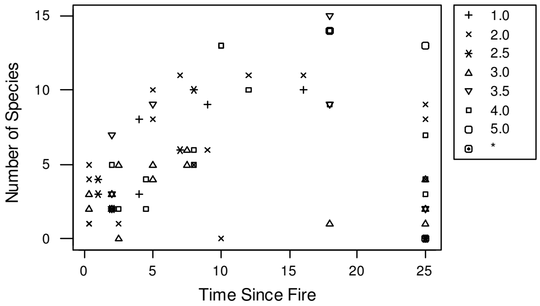
APPENDIX 9

The graphs below relate the following covariants to the changes in lichen diversity following burning: altitude, slope, fire intensity and stage when burnt.

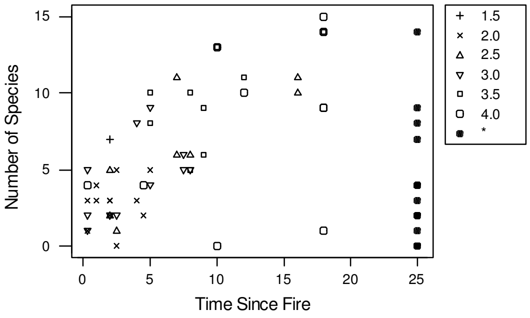
Lichen Diversity Since Burn Related to Altitude



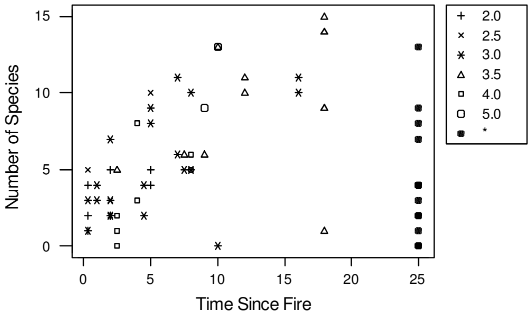
Change in Lichen Diversity Following Burn Related to Slope



Change in Lichen Diversity Since Burn Related to Fire Intensity

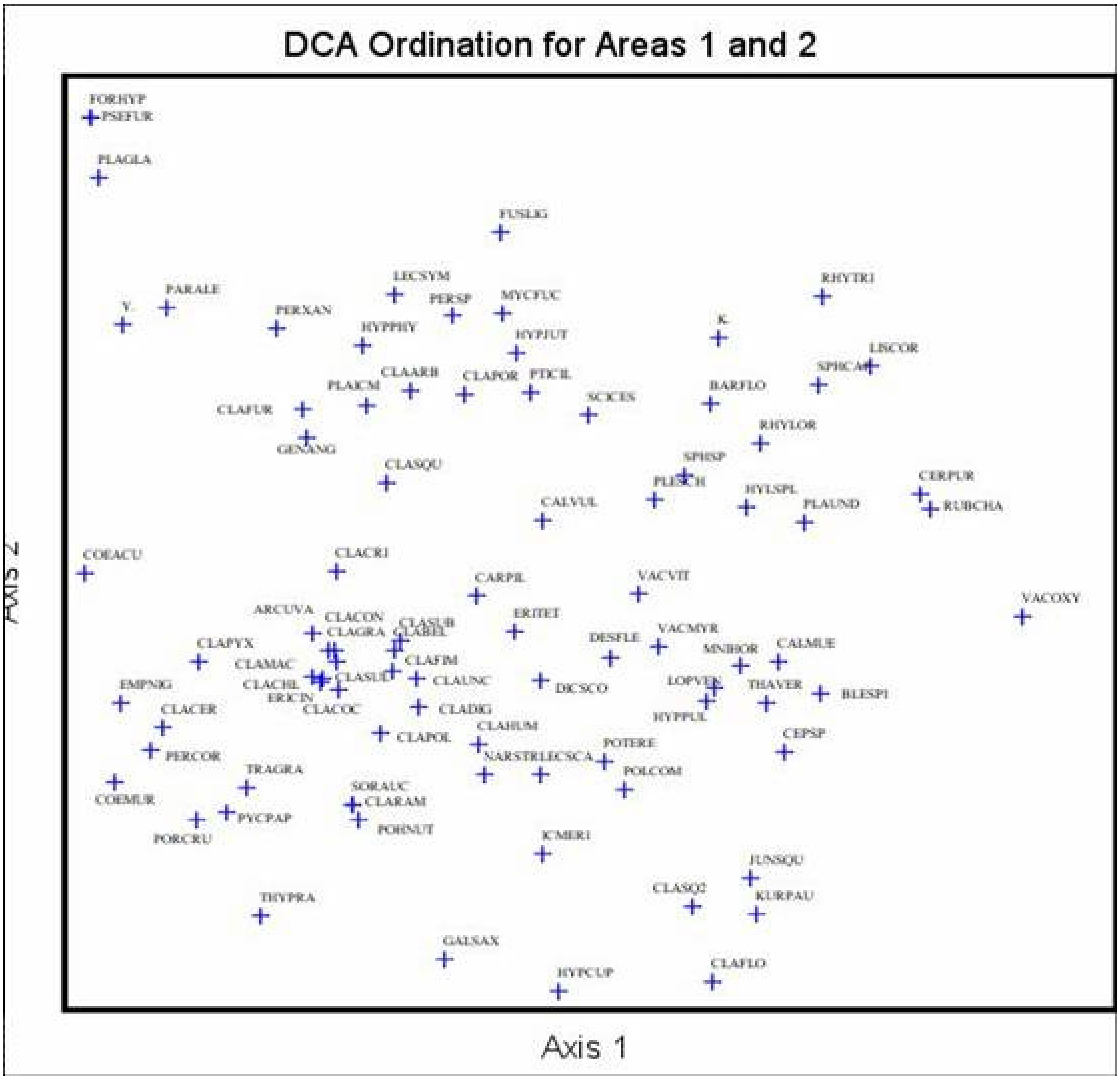


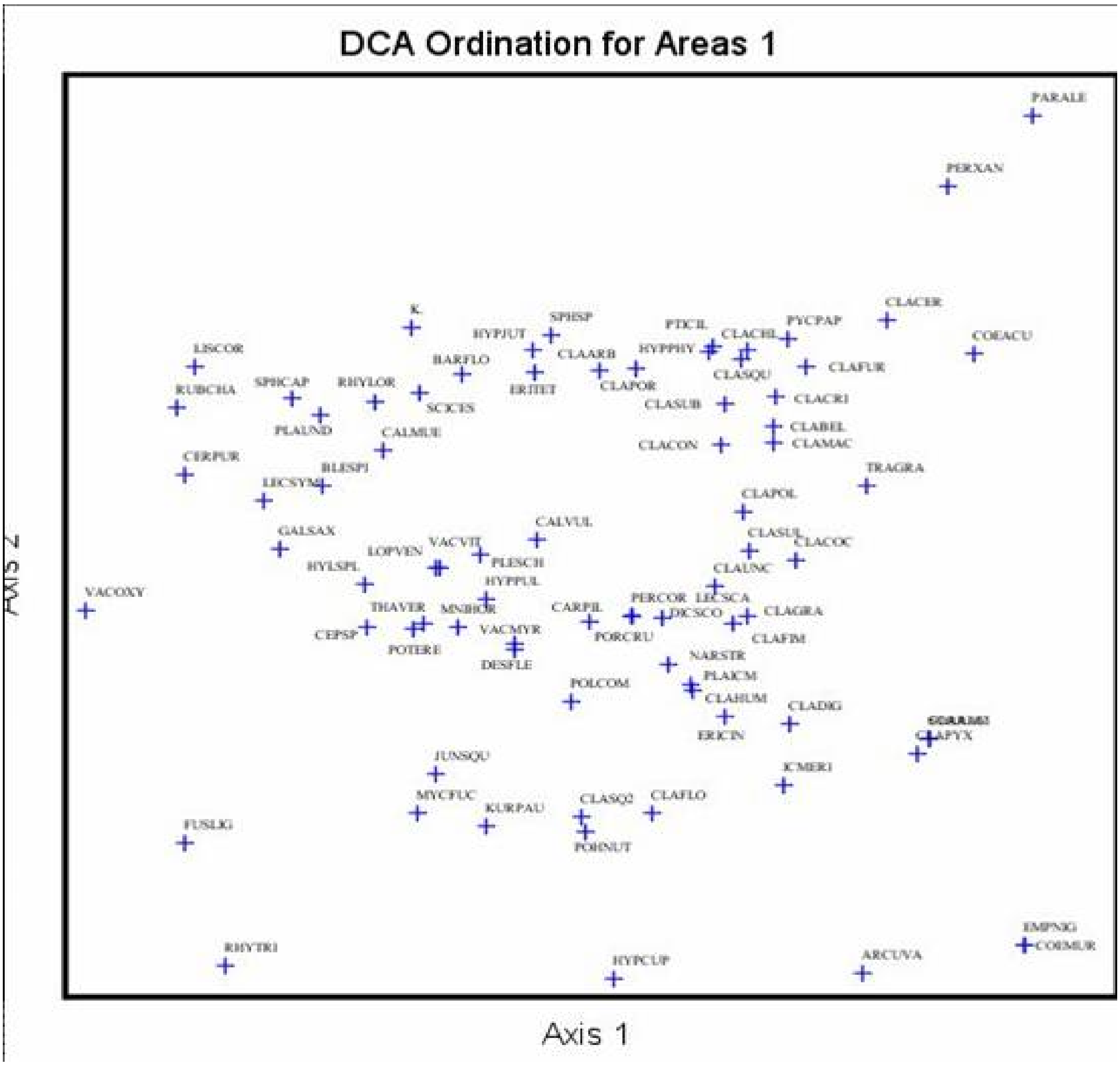
Change in Lichen Diversity Since Burn Related to Age When Burnt

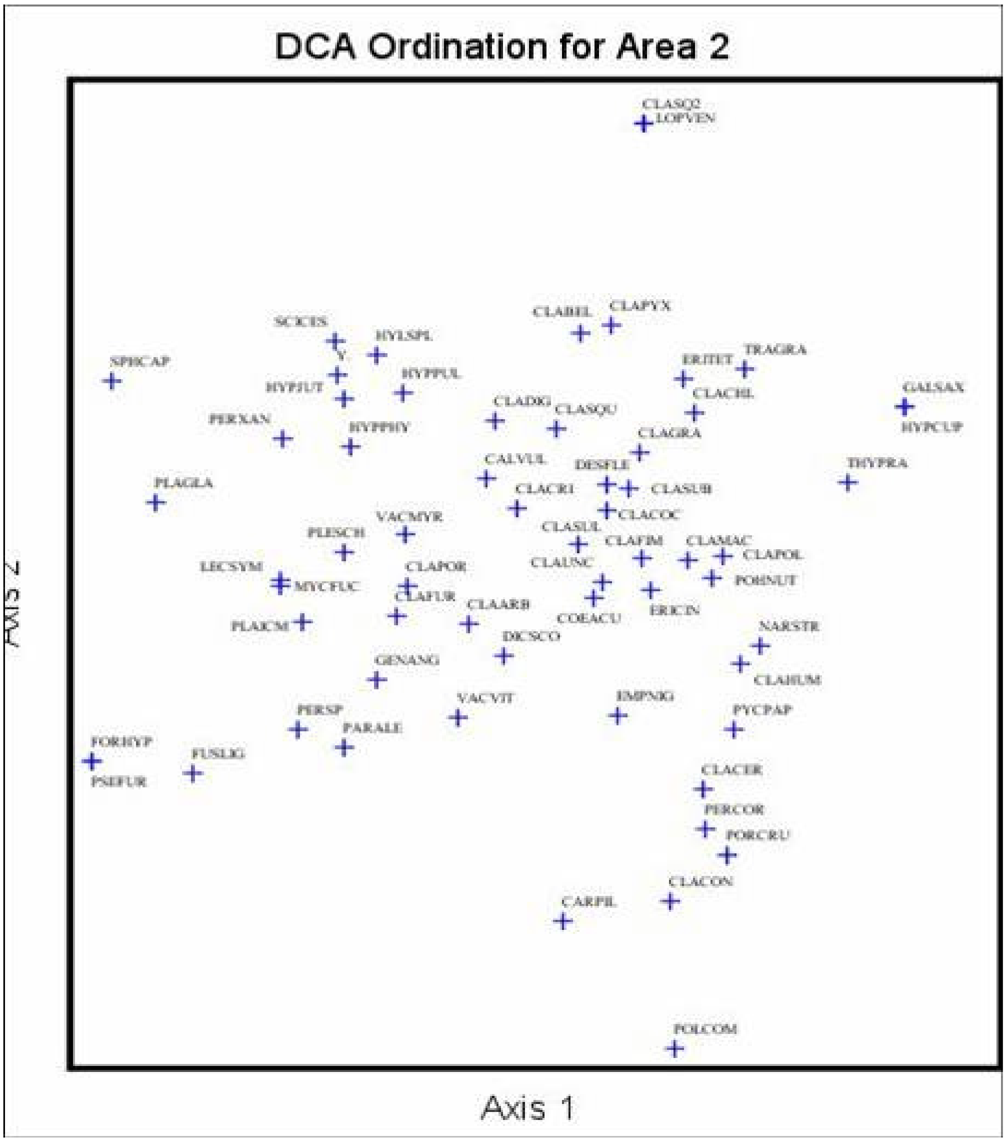


APPENDIX 10

Species Ordination Plots




DCA Ordination for Areas 1
Axis 2
Axis 1
PARALE
PERXAN
CLACER
COEACU
K.
SPHSP
HYPJUT
PTICIL
CLACHL
PYCPAP
LISCOR
BARFLO
CLAARB
HYPPHY
CLAFUR
CLASQU
RUBCHA
SPHCAP
RHYLOR
ERITET
CLAPOR
SCICES
CLASUB
CLACRI
PLAUND
CLABEL
CALMUE
CLACON
CLAMAC
CERPUR
BLESPI
TRAGRA
LECSYM
CLAPOL
CALVUL
GALSAX
CLASUL
VACVIT
CLACOC
LOPVEN
PLESCH
HYLSPL
CLAUNC
HYPPUL
VACOXY
PERCOR
LECSCA
THAVER
MNIHOR
CARPIL
DICSCO
CLAGRA
CEPSP
VACMYR
PORCRU
CLAFIM
POTERE
DESFLE
NARSTR
POLCOM
PLAICM
CLAHUM
CLADIG
ERICIN
CLAPYX
JUNSQU
ICMERI
MYCFUC
KURPAU
CLASQ2
CLAFLO
FUSLIG
POHNUT
EMPNIG
RHYTRI
COEMUR
HYPCUP
ARCUVA


DCA Ordination for Area 2
CLASQ2
LOPVEN
CLABEL
CLAPYX
SCICES
HYLSPL
Y
SPHCAP
ERITET
TRAGRA
HYPJUT
HYPPUL
CLACHL
GALSAX
CLADIG
CLASQU
HYPCUP
PERXAN
HYPPHY
CLAGRA
CALVUL
DESFLE
THYPRA
PLAGLA
CLACRI
CLASUB
CLACOC
VACMYR
PLESCH
CLASUL
CLAFIM
CLAMAC
CLAPOL
CLAUNC
LECSYM
CLAPOR
POHNUT
MYCFUC
CLAFUR
CLAARB
COEACU
ERICIN
PLAICM
NARSTR
DICSCO
GENANG
CLAHUM
VACVIT
EMPNIG
PERSP
PYCPAP
PARALE
FORHYP
FUSLIG
PSEFUR
CLACER
PERCOR
PORCRU
CLACON
CARPIL
POLCOM
Axis 2
Axis 1